BIOGEOGRAPHY AND CONSERVATION OF TERRESTRIAL AFROTROPICAL BIRDS

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To my mother and grandparents

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DISCLAIMER

I declare that this thesis is my own unaided work, both in concept and execution, and that apart from the normal guidance from my supervisor, I have received no assistance, except as acknowledge in the acknowledgements section, and has not been submitted to any other university.

Signed by candidate

H. M. de Klerk

ABSTRACT

This study aimed to describe patterns of distribution in terrestrial Afrotropical birds, to investigate the causes of these patterns, and examine how aspects of distributional patterns may be used to prioritize local regions for conservation attention.

Presence-only data were gathered and digitized at one-degree square scale for the 1686 terrestrial bird species that breed on or regularly visit subSaharan Africa as non-breeding migrants. Biogeographical analysis of the 1437 species that are globally restricted to subSaharan Africa (Afrotropical endemics) revealed a suite of geographical areas that have a homogenous and characteristic avifaunal composition, termed avifaunal zones. The approach used in this study ensured representativeness in the resultant biogeographical classification scheme, which was not biased towards avifaunas that are species rich or that contain many narrow endemics, and further included avifaunas that consisted of few, but taxonomically and ecologically distinct species (e.g. the Namib Province). Analysis of zonal boundaries exhibiting high levels of turnover, defined specifically as species replacement, were distinguished from zonal boundaries that are characterised by species richness gradients. For instance, the northern forest-savanna boundary between the Guineo-Congolian and Northern Savanna Subregions was shown to consist of a sharp ecotone between forest and savanna, whereas the boundary between the Northern Savanna and Northern Arid Subregions was shown to be dominated by species drop-outs. This shows that whereas the Northern Savanna Subregion represents a unique avifauna that is distinct from that of the Guineo-Congolian Subregion, the Northern Arid Subregion is merely a depauparate subset of the Northern Savanna avifauna.

Patterns of species richness and narrow endemism where shown to differ between species groups that exhibit different life history characteristics (e.g. residents vs. migrants) and distributional characteristics (e.g. Afrotropical endemics vs. nonendemics). Differences can probably be attributed to island biogeography and areography theory.

The question as to what the relative roles of the current environment and history events (such as historical climatic oscillations, and formation of mountains, rivers and lakes) have been in shaping distributional patterns of birds in subSaharan Africa is confounded by a number of factors. However, the importance of environmental stability (both inter- and intra-annual) in determining species richness and

concentrations of narrow endemics was clearly demonstrated. For instance, stability (or reliability) of current environmental factors, whether it be rainfall, temperature or productivity, is strongly and significantly correlated with both high species richness and concentrations of narrow endemics. It is quite likely that current inter-annual stability is linked to localised areas that were climatically stable over longer term cycles.

Areas showing local climatic stability may not only be important to conservation because of their ability to protect species over the long term and due to their probable roles as centres of speciation. Such areas may also be important to conservation, because, in a number of subregions, they contain nested biotas. For instance, in the Guineo-Congolian Subregion, proposed refugia not only show co-occurrence of narrow endemics, but also coincidence of peaks of species richness with peaks of narrow endemics. This facilitates efficient placement of priority areas in conservation planning. Co-occurrence of narrow endemics implies that few irreplaceable grid cells (that is grid cells selected to represent narrow endemics) are needed in a near minimum set determined by complementarity analysis to represent all species in a given data set. A reduction of the number of irreplaceable grid cells allows the complementarity algorithm greater freedom in siting of grid cells in order to increase efficiency (measured here as the number of grid cells needed to represent all species). Coincidence of peaks in species richness with peaks of narrow endemism means that inflexible choices of grid cells selected to represent narrow endemics also contain many wider ranging species, representing high total numbers of species. This reduces the set size. The Northeastern Subregion represents an avifauna with low levels of nestedness. As a consequence, a relatively large number of grid cells are needed to represent few species. Low levels of nestedness in the Northeastern avifauna may well be due to the lack of larger highland-lowland refugium complexes. Stability in the Northeastern Subregion is more likely to have been localised in small localities scattered throughout the Ethiopian Highlands and associated foothills (which have complex topography and may provide local amelioration of climatic conditions).

Results of this thesis demonstrate a complex interplay between current and historical environmental stability with patterns of distribution of Afrotropical birds. This interaction affects choice and efficiency of techniques used to develop priorities for the selection of areas in which to focus conservation attention aimed at Afrotropical bird species.

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CHAPTER 1. General Introduction

Opportunity costs, that is the lost value of the next best option (e.g. Mohr & Fourie 1995, Perman *et al.* 1996), necessitate careful planning in all decision-making arenas. Efficient decision-making requires a framework. A biogeographical framework provides an appropriate tool for investigating biological aspects of conservation decision-making as it studies patterns of biological distribution and diversity, and ensures a dualistic perspective. Although some authors argue for either an ecosystem-based (e.g. Walker 1992, Lapin & Barnes 1995) or species-based approach, dualistic approaches with an emphasis on the interdependence of species and ecosystems (e.g. Noss 1983) are more pragmatic (e.g. Dasmann 1972, Udvardy 1975, Noss 1987, 1990, Collar *et al.* 1994, Lombard 1995). A hierarchical biogeographical classification based on species and ecosystems provides a framework for the identification of floras and faunas that require conservation measures (Dasmann 1972, 1973, 1974, Udvardy 1975). Knowledge of species distributions, patterns of species richness and endemism, and the processes that drive them facilitate conservation decision-making and priority setting (Rebelo & Siegfried 1990, Gelderblom *et al.* 1995, Williams *et al.* 1996a). For instance, the degree of biogeographical zonation of a region by its flora or fauna indicates the variety of areas needed to conserve maximum diversity (Turpie & Crowe 1994). In addition, a biogeographical framework ensures representativeness (e.g. Emanuel *et al.* 1992, Turpie & Crowe 1994) and helps to avoid the conservation of species at the margins of their range (e.g. Gelderblom *et al.* 1995). Indeed, the development of conservation priorities in a vacuum of biogeographical understanding may lead to invalid comparisons of priorities between biota of very different biogeographical regions (Turpie 1995).

To date there have been two publications dealing with conservation priorities for birds on a regional (or larger) scale for subSaharan Africa, neither of which have taken a biogeographical approach. Collar *et al.* (1994) specifically aim to identify and document threatened species that merit conservation attention through the application of IUCN Red Data Book categories. 'Birds to watch 2' (Collar *et al.* 1994) admirably meets this goal. BirdLife International's Endemic Bird Area (EBA) programme aims to 'identify priority areas for the conservation of global biodiversity' by focussing on range-restricted taxa and by using birds as indicators (ICBP 1992). The EBA programme was based on Terborgh and Winter's (1983) study on siting protected areas in Columbia and Ecuador. In this study, Terborgh and Winter (1983) suggested that species with small ranges constituted priorities, as they are most susceptible to

habitat destruction. Terborgh and Winter (1983) defined a 'small range' as one that is less than 50,000km^2. The EBA program modified this definition slightly to specify a range-restricted species to be one that has a *historical* breeding range of less than 50,000km^2 (ICBP 1992). Coincidence of two or more such range-restricted species constitutes an EBA (ICBP 1992). The EBA is an admirable and successful effort for identifying areas that are important for the conservation of range-restricted bird species. However, concern has been expressed that the restricted-range species definition necessarily precludes large-bodied wide-ranging species (Keast 1994), certain of which may well have smaller global population sizes than many range-restricted species (Kratter 1993). In particular, the definition misses avifaunas that are reliant on resources that are patchily dispersed over the landscape or ephemeral. Such species may narrowly miss the critical cut-off, or they may have a range of less than 50,000km^2 within any one year, but over the years accumulate a range larger than this critical limit (Crowe 1993, Crowe & Brooke 1993). An example are the mobile, arid adapted bird species, which must shift their ranges from year to year as they track rainfall events (Little *et al.* 1996). This highlights that a single cut-off approach is inappropriate to almost any conservation prioritisation or biogeographical methodology on a sub-continent that has many and varied types of biomes, each of which will demand vastly different life history strategies from their respective inhabitants.

Existing biogeographical studies of birds of subSaharan Africa (the Afrotropics) are either based on distributional data compiled more than two decades ago (e.g. Chapin 1932 and references therein, Crowe & Crowe 1982), and/or only focus on a portion of the avifauna or region (Winterbottom 1978, Diamond & Hamilton 1980, Clancey 1986, Muriuki *et al.* 1997). Consequently, this thesis sets out to re-assess Afrotropical avifaunal biogeography, specifically for terrestrial species, to provide a detailed and current framework for the identification of *local regions* important for the conservation of terrestrial birds within the Afrotropics. To this end, new data and some new analytical procedures are applied and results are corroborated through a synthesis of much of the work previously published on aspects of bird distribution in the Afrotropics. More specifically, the aims of this research are:

1. to describe biogeographical patterns of Afrotropical birds, including patterns of species richness (diversity), narrow endemism and distribution,
2. to determine probable correlations between current environmental variables and these patterns to elucidate the respective roles of the extant environment and history in the development of these patterns,

3. to utilize this information to identify local regions of conservation priority for terrestrial Afrotropical birds.

Thesis layout

Data used and rationale behind the decisions as to what type of distributional data and taxonomic arrangement to be used in this study are outlined in detail in Chapter 2.

Chapters 3 and 4 describe general patterns and peaks of species richness and narrow endemism (as measured by two indices of range-size) and investigate possible relations between these patterns and current environment variables. An attempt is made to elucidate the amount of variability in patterns of species richness accounted for by the current environment. Chapter 4 also investigates differences in environmental correlates of species richness between species groups that represent different life history strategies (resident vs. migratory) and distributional characteristics (centred within subSaharan Africa, or centred to the north of subSaharan Africa).

Chapter 5 investigates patterns of distribution of terrestrial birds restricted to subSaharan Africa, specifically, the occurrence of regions of distinct avifaunal composition. These patterns are discussed in the light of results obtained in detailed published field studies. Possible roles of current environment and vicariant speciation in determining these patterns are highlighted.

The implications of the results obtained in Chapters 3 to 5 on conservation prioritisation exercises are outlined in Chapter 6. In particular, the effect of nestedness of distributional patterns (of both species richness and richness of narrow endemics) on the size of near minimum sets required to represent all species at least once in a particular avifaunal subregion, is investigated.

Chapter 7 provides a synthesis of the analyses and results of Chapters 3 to 6, particularly concentrating on the investigation into causes of patterns.

CHAPTER 2. Study region and bird species data

2.1. Region and scale

The study area comprises continental Africa south of 20°N, termed subSaharan Africa (e.g. IUCN 1990), or the Afrotropical region (*sensu* Udvardy 1975:25) (previously the Ethiopian region *sensu* the Sclater-Wallace system: Wallace 1876). The use of this study region is in keeping with many studies on biogeography (e.g. Chapin 1923, 1932; IUCN 1990), speciation (e.g. Hall & Moreau 1970; Snow 1978) and conservation (Udvardy 1975; IUCN 1986, 1987, 1990), for flora (Keay 1959), as well as fauna (Burgess *et al.* in press). The flora and fauna of the Sahara and north Africa, are usually considered to be Palaearctic rather than Afrotropical in nature (e.g. Dowsett & Forbes-Watson 1993). The few works that have considered Africa as a whole, at once argue that excluding north Africa misses much that is of interest to the biologist (Moreau 1966; followed by Brown *et al.* 1982; a point contested by Rowan 1984), but admit that 'the bird fauna of North Africa is overwhelmingly Palaearctic in affinity' (Brown *et al.* 1982:13).

Yemen on the southern tip of the Arabian peninsula is variably included (e.g. IUCN 1986; Maclean 1990; Dowsett & Forbes-Watson 1993) or excluded (e.g. Hall & Moreau 1970; Udvardy 1975; IUCN 1987) in the Afrotropical region. Hall and Moreau (1970:v) state that they consider this minor extension of range "not important for analysis of speciation patterns within Africa" which reasoning is followed for the purposes of this study.

Speciation, biogeography and conservation strategies for islands represent a special case, being affected by different forces to those acting on a continent (e.g. Hall & Moreau 1970:ix). As a result, islands are sometimes even considered to be a separate subregion (Pomeroy & Ssekabiira 1990). In agreement with many studies that suggest that, due to the aforementioned reasons, island and continental situations be analysed and dealt with separately (e.g. Pomeroy & Ssekabiira 1990), this study does not include islands.

SubSaharan Africa was divided into 1961 1 x 1 degree squares (approximately 110 km x 110 km; Fig. 2.1). The latitudinal variation in the area extent of these grid cells is relatively small (e.g. Williams *et al.*

1996b). However, it must be noted that the area extent of many coastal grid cells will be somewhat smaller, and that of grid cells encompassing mountains somewhat larger, than average. This scale was chosen in keeping with the presumed level of accuracy in the most poorly sampled areas (see below).

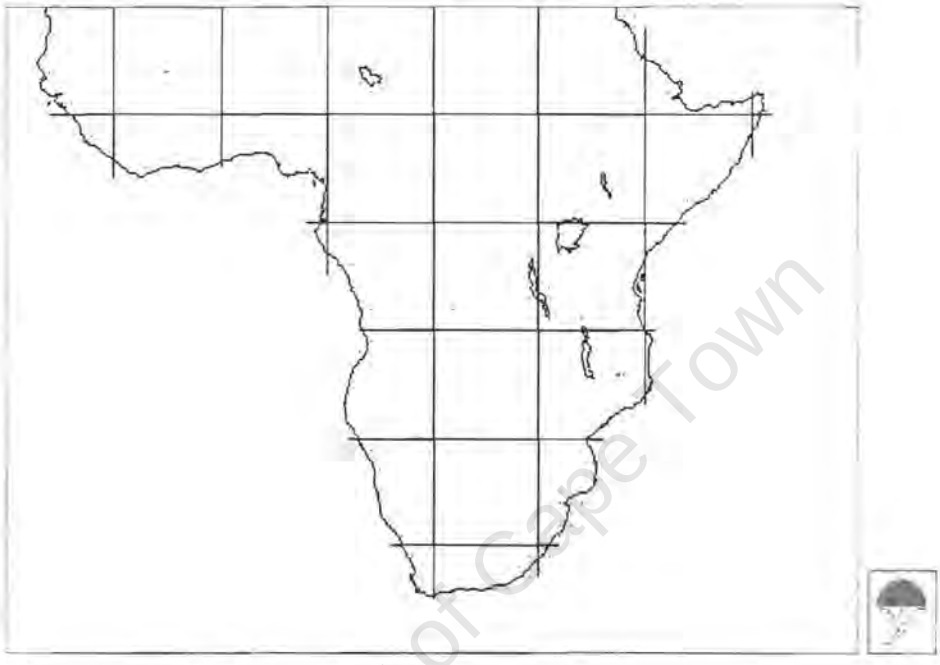


Figure 2.1. The 1 x 1 degree square grid cell system used to digitise data for subSaharan Africa (1961 grid cells).

2.2. Taxonomy

Taxonomy follows Sibley and Monroe (1990) as it is one of only two complete, recent works covering all birds occurring in the Afrotropics. The second work is that of Dowsett and Forbes-Watson (1993), which is based on the taxonomy presented in Dowsett and Dowsett-Lemaire (1993) (henceforth jointly referred to as the "Dowsett compilations"). Sibley and Monroe (1990) is based on the work of Sibley and Ahlquist (1990) (henceforth jointly referred to as the "Sibley compilations"). Specific taxonomic decisions in both the Sibley and the Dowsett compilations are contested (see Elgood 1994; Stuart 1995; and references cited below), as will be the case with any new classification. The Sibley compilations were chosen despite numerous criticisms (e.g. Raikow 1991; Krajewski 1991; O'Hara 1991; Peterson

1992, for reviews of Sibley & Ahlquist 1990; Siegel-Causey 1992 for a review of Sibley & Monroe 1990) as they *aim* to apply a phylogenetic species concept (although this is contested by Peterson 1992; C. Rahbek pers. comm.; J. Fjeldså pers. comm.). The Dowsett compilations, in contrast, are based explicitly on the biological species concept (Dowsett & Forbes-Watson 1993:6), a deficiency pointed out by Brooke (1994). The biological species concept tends to recognize fewer species (Hall & Moreau's 'lumpers', 1970), which has implications for both biogeographical and conservation studies. Subsuming multiple taxa into a single species, each of which has its own history of speciation (Barrowclough 1992), could disguise informative patterns of distribution and speciation. This could lead to the species richness of particular areas being underestimated, and could preclude the conservation of individual taxa that are lumped within a biological species from being specifically accounted for.

Hall and Moreau (1970) define members of superspecies as those assumed to be immediately descended from a common ancestor, which, in addition, are completely or nearly, parapatric or allopatric. This study follows Sibley and Monroe (1990) in the assignation of superspecies membership, which is indicated with square brackets. For instance, *Eremomela* [*badiceps*] *badiceps* and *Eremomela* [*badiceps*] *turneri* are two sister species in the superspecies '*badiceps*'.

2.3. Species included in the database

According to the taxonomy of Sibley and Monroe (1990, 1993), 1646 terrestrial bird species breed on the mainland of subSaharan Africa or regularly visit this region as non-breeding migrants (either from the Palaearctic or Madagascar) (labelled BB, PM and MM respectively in Appendix 2.1). Distributional information for these 1646 terrestrial bird species was collected from various published sources (Appendix 2.2). Occurrence within the Afrotropics was based on distributional information presented in Sibley and Monroe (1990, 1993), Dowsett and Forbes-Watson (1993) and the Handbooks of the Western Palaearctic (volumes I – IX, see Appendix 2.2 for individual references). Waterbirds, defined as those species that are dependent on non-marine aquatic biotopes for feeding, breeding (*sensu* Guillet & Crowe 1985) and/or roosting, were excluded form analysis, as they have been shown to have different distributional patterns to those of terrestrial species (Moreau 1966; Guillet & Crowe 1985) (see Appendix

2.3 for a list of Afrotropical species defined as waterbirds according to the aforementioned definition). Pelagic species, defined as those that do not breed, roost or feed on the continental mainland (Appendix 2.4), were specifically excluded, as were vagrant species that, according to Dowsett and Forbes-Watson (1993), have been only recorded incidentally in the region (Appendix 2.5).

Terrestrial birds occurring in the Afrotropics fall into a number of life history categories (Table 2.1). Species can be resident (sedentary or exhibit localized movement over short distances), intra-African migrants, or inter-African migrants, which are chiefly from the Palaearctic. Intra-African migrants were not separated out from sedentary species as insufficient data are currently available to enable rigorous definition and mapping of such species. Most Palaearctic migrants are non-breeding, but 15 species have local populations that breed in the Afrotropics (e.g. *Egretta garzetta*, *Plegadis falcinellus*, and *Sterna albifrons*, labelled BP in Appendix 2.1). Accurately separating out distributional records of resident populations from those for migrant populations proved to be difficult, and so the locally resident populations of these 15 species have been classified along with the migratory populations as Palaearctic migrants. Lastly, resident species can have their entire global range restricted to the Afrotropics (termed '*endemics*' in this study), be centred in the Afrotropics but extending some distance beyond the bounds to include North Africa (e.g. Moreau 1966; followed by Brown *et al.* 1982), southern Arabia (e.g. IUCN 1986; Maclean 1990; Dowsett & Forbes-Watson 1993), Madagascar, or the islands of Comoro, Aldabara, Seychelles and Socotra (P.A.R. Hockey pers. comm.), or be centred outside of the Afrotropics, but extending to some degree into the Afrotropics. Combinations of these life history and distributional traits form a number of classes (see Table 2.1). Although nonpasserines do not represent a monophyletic group, the endemic terrestrial database was split into nonpasserines (427 species) and passerines (1010 species) as the latter have possibly been subject to different selection pressures (Moreau 1966). While some authors postulate that the diversity of passerines represents a recent (Pleistocene) and currently active radiation (Moreau 1966, Pomeroy & Ssekabiira 1990), recent molecular studies suggest that passerines might be much older and may not be monophyletic (J. Fjeldså pers. comm.).

Table 2.1. Life history and distributional categories used to derive analysis groupings. ES = globally restricted to the Afrotropical region (NP = nonpasserines and P = passerines), ER = distribution centred in Afrotropical region but extending out of the Afrotropics, NE = distribution centred outside the Afrotropics but extending into the Afrotropics, BP = Palaearctic migrants to the Afrotropics that have local breeding populations within the Afrotropics, PM = Palaearctic migrants, and MM = migrants from Madagascar.

Breeding residents	ES	NP	①	497	③	1437 (all endemics)	⑥ 1534 (all residents)	⑦ 1646 (all terrestrial species)
		P	②	1010				
	ER			47	④	97 (all nonendemic residents)		
	NE			50				
Migrants	BP			15	⑤	112 (all migrants)		
	PM			96				
	MM			1				

2.4. Distributional data - ideal data versus availability

Ideal data for both biogeographical and conservation studies should consist of presence and confirmed absence data in the form of point or locality data, together with abundance and population trend data (e.g. Harrison 1989) that have been derived from even sampling effort across the entire region under study. Compilations of distributional data for birds in subSaharan Africa are available in point format (Hall & Moreau 1970; Snow 1978, hence forth collectively referred to as the "Atlases of Speciation"), range map format for some species (Brown *et al.* 1982; Urban *et al.* 1986; Fry *et al.* 1988; Keith *et al.* 1992; Urban *et al.* 1997, hence forth referred to as the "Birds of Africa") and atlas format for certain parts of the region, (e.g. Lewis & Pomeroy 1989; Harrison *et al.* 1997). These different data types all have inherent shortcomings.

Point and atlas data suffer from bias in sampling, or recorder, effort as areas may be preferentially targeted due to proximity to major population or educational centres, ease of access, scenic beauty or protected status, whilst species may be preferentially targeted because they are charismatic or rare, or they may be consistently over-looked due to inconspicuous appearance, cryptic habits (e.g. skulkers and nocturnal species) or low densities (for good discussions see Prendergast *et al.* 1993a; Freitag & van Jaarsveld 1995; Gelderblom & Bronner 1995; Robertson *et al.* 1995). Sampling effort is also affected by time of day, season and weather conditions (Prendergast *et al.* 1993a), and specifically in the case of volunteer driven atlas projects, by the amount of time spent sampling, *a priori* knowledge of an area

(Gibbons *et al.* 1993; Robertson *et al.* 1995) and variable ability and experience of individual recorders (e.g. Prendergast *et al.* 1993a).

Sampling effort bias causes two types of error in the resultant data, namely under-sampling and over-sampling. Under-sampling occurs in areas that are neglected by data collectors (for reasons outlined above) leading to 'errors of omission' when species are not recorded in areas where they do in fact occur (e.g. Gelderblom & Bronner 1995). Under-sampling can result in potentially diverse areas being overlooked. Certain *species* can also be under-sampled and may consequently appear to be scarcer in the database than they truly are (Freitag & van Jaarsveld 1995), both in terms of range-size and abundance. Over-sampling results from the inclusion of rare visitors and vagrant species in species lists for very well sampled areas that 'may not be considered meaningful in relation to the actual biological community of the area' (Harrison & Martinez 1995:410). Over-sampling is particularly problematic in mobile taxa such as birds, and perhaps even more of a problem in biological databases aimed at conservation priority setting than under-sampling, as it may encourage 'over-optimism' with regard to the conservation potential of over-sampled areas (Harrison & Martinez 1995). Over-sampling can also occur in range map data (see below).

As specimen collecting has become less popular over the last few decades (Snow 1978; Winkler 1996), point databases must rely heavily on sight-based records. Problems can arise with unpublished sight records if they are included uncritically in the database (e.g. Hall & Moreau 1970). The trend not to 'collect specimens' creates a particular problem for cryptic species that are often difficult to identify 'out of hand' (i.e. without having the bird in hand). Such cryptic species may be mis-identified (Snow 1978) and be under-represented in the database. Much point data, particularly that based on specimens, may be out of date (e.g. Hall & Moreau 1970), particularly if large scale habitat alteration (Gelderblom & Bronner 1995) or species exploitation has occurred subsequent to collection (Scott *et al.* 1993). Again, these problems can also affect range maps (Freitag & van Jaarsveld 1995).

As point data for birds in Africa suffer quite heavily from sampling bias (mainly in the form of under-sampling) and some are out of date, point data need to be treated to reduce such biases. A number of

methods that correct for sampling effort for both point and atlas data for use in diversity and conservation assessments, such as smoothing (Prendergast *et al.* 1993a) and diversity indices (Harrison & Martinez 1995), result in the loss of information about individual species present in specific localities (Harrison & Martinez 1995; Williams *et al.* 1996b). Range maps represent an attempt to model expected distributions of *individual* species in order to overcome problems of under-sampling in areas where funds and expertise are limited or lacking. Techniques employed vary from simple 'range-fill' maps that are generally created by extrapolating species ranges from point data along vegetation boundaries with little consideration for real gaps in this extent of occurrence (Scott *et al.* 1993; Freitag & van Jaarsveld 1995), to sophisticated statistical procedures that provide probabilities of occurrence of species based on detailed knowledge of a species' habitat requirements and specificity (e.g. Margules & Stein 1989; Tushabe *et al.* submitted; see Williams *et al.* 1996b for discussion of various techniques). The less rigorous methods of range modelling (particularly the coarse range-fill approach) often suffer from 'errors of commission'. An error of commission occurs when a species is recorded as being present in an area where it may in fact not occur (e.g. Gelderblom & Bronner 1995). Range maps derived from statistical modelling substantially improve upon the problem of errors of commission that may arise from coarse range-interpolation. Unfortunately, however, detailed information on habitat requirements for many species currently remain scant to non-existent. For example, whils. the general range of intra-African migrants may be known (with some degree of certainty), aspects of habitat requirements (e.g. Rudd's lark *Heteromirafra ruddi*, P.G. Ryan pers. comm.), breeding grounds (e.g. Spotted Ground Thrush *Turdus fischeri,* Lewis & Pomeroy 1989:375) or movements (e.g. Grey-Rumped Swallow *Hirundo griseopyga*, Lewis & Pomeroy 1989:320) are often lacking. This highlights the urgent need for ecological studies and the collection of distribution data (Lewis & Pomeroy 1989). Of course, in addition to errors of commission, uncritical use of point data that show uneven coverage of a region, or which are dated, to develop range maps, irrespective of techniques used, can lead to the resultant range maps suffering from the same problems (Williams *et al.* 1996b).

The decision as to what data to use boils down to a trade-off between the various types of biases outlined above. Some authors argue that, for conservation purposes, errors of commission resulting from range-fill maps are unacceptable as the risk arises that species are considered to be protected in areas where

they in fact may not occur (e.g. Freitag & van Jaarsveld 1995; Gelderblom & Bronner 1995). However, a similar problem can manifest in point data from over-sampling (Harrison & Martinez 1995). Under-sampling or incomplete data derived from point localities can also yield misleading results that have serious implications for biogeography and conservation studies (Kodric-Brown & Brown 1993). Studies that compare conservation priorities derived using identical methods on both point and range map data yield somewhat conflicting results. While some show that use of range maps can be seriously misleading (Freitag & van Jaarsveld 1995; Freitag *et al.* 1996), others show that the differences may not always be that great (Gelderblom & Bronner 1995; Freitag *et al.* 1997), depending on how carefully the range map data are developed and used (Scott *et al.* 1993; Gelderblom & Bronner 1995). Discrepancies between point and range map data will vary according to the taxon under consideration, being less likely to be problematic with more mobile taxa, as was shown to be the case for birds in Idaho (Scott *et al.* 1993).

As a result of the constraints of large gaps in point data for the Afrotropics, particularly in some of the former French territories in West Africa, northern Mozambique and eastern Angola (Hall & Moreau 1970), it was decided to use *conservatively* developed range maps based on point data presented in the Atlases of Speciation and numerous other published sources (see Appendix 2.2) using current knowledge of habitat requirements and specificity. Careful attention was paid to possible discontinuities in ranges due to local habitat changes (e.g. the dry Zambezi valley which provides a real break in many species ranges that otherwise occur widely throughout the Zambezian miombo woodland; see Benson *et al.* 1962 for example) and naturally patchy distributions of certain species (e.g. *Heliolais erythroptera* and *Apalis alticola*). In the latter case, species were mapped as localities, as were species with very restricted ranges. As suggested by a number of authors (e.g. Gelderblom & Bronner 1995; Williams *et al.* 1996b), range maps are viewed as *potential* distributions, which should not be taken as confirmed presence data. Consequently results of this study aim only to describe probable biogeography and highlight areas potentially important for the conservation of Afrotropical birds. Such areas should be studied at finer scale and ground-truthed before action is recommended or taken.

2.5. Species habitat data

Habitat information for the bird species was extracted chiefly from Sibley and Monroe (1990, 1993), Mackworth-Praed and Grant (1952-73), Serle *et al.* (1977), Sinclair *et al.* (1993) and Zimmerman *et al.* (1996).

2.6. Digitisation

WORLDMAP software (ver. 4.17.01, Williams 1997) was used to digitise individual bird distributions into the one-degree grid cell system. ARC/INFO (ver 6.1.1., Environmental Systems Research Institute, Redlands, California) was used to create the various species group subsets.

CHAPTER 3. Patterns of species richness and narrow endemism

Summary

Patterns and peaks of species richness for all terrestrial bird species, terrestrial residents, all Afrotropical endemics (species that are globally restricted to subSaharan Africa), endemic passerines and endemic nonpasserines, and patterns and peaks of narrow endemism (only calculated for all Afrotropical endemics, endemic passerines, and endemic nonpasserines) occur along the mountains of the Albertine Rift, southern Kenya, northern Tanzania, the Eastern Arc of central Tanzania, Nyika, Viphya, Malanje and Chimanimani of eastern and southern Africa, and Loma, Macent, Nimba, and the Cameroon-Bameda Highlands of western Africa. Additional species richness peaks not highlighted in these species groups by measures of narrow endemism occur in the lowlands of the northeastern Congo basin (Ituri). Additional peaks of narrow endemism not highlighted in these species groups by species richness occur in the Ethiopian Highlands (particularly for nonpasserines) Angolan Escarpment, Katanga Plateau, and in Somalia (particularly for passerines), and the lowlands adjacent to the Cameroon-Bameda Highland system.

Within Afrotropical endemics, passerines and nonpasserines show largely similar patterns of species richness and narrow endemism, with only a few differences observed (outlined above). This is contrary to suggestions that patterns for passerines and nonpasserines differ significantly due to differences in speciation history (Moreau 1966; Pomeroy & Ssekabiira 1990). Within residents, patterns of species richness vary greatly between Afrotropical endemics (which concentrate in montane forests and southern Brachystegia woodlands) and nonendemics residents (which concentrate in Sudanian woodlands and the Ethiopian Highlands). Patterns of species richness of residents and inter-African migrants also show notable differences. Residents show patterns similar to those of Afrotropical endemics, while migrants show patterns similar to those of nonendemics.

Patterns and peaks of species richness and narrow endemism within Afrotropical endemics show coincidence in montane forests. However, a number of differences occur (as outlined above).

3.1. Introduction

Patterns of species richness are useful in descriptive biogeography and in conservation prioritization exercises in two ways. Firstly, patterns of richness provide a simple representation of how distributional patterns differ according to distributional characteristics (e.g. endemic residents vs. nonendemic residents) and life history strategies (resident vs. migratory) of species under consideration. Secondly, patterns of species richness and, in particular, peaks in richness highlight areas that currently probably have a high carrying capacity, and *may* give clues to the possible existence and localities of areas that have possibly allowed species to accumulate due to stability over the medium term (Fjeldså 1994; Fjeldså & Lovett 1997) to long term (*viz.* Pleistocene refugia *sensu* Haffer 1969; Diamond & Hamilton 1980; Crowe & Crowe 1982), but see Tuomisto and Ruokolainen (1997) for problems involved in investigating historical events based on current distributions.

It is also important to look at the distribution of endemic species as the notion that endemics require special protection is wide spread (e.g. Drinkrow & Cherry 1995; Gelderblom & Bronner 1995). First, endemics are usually, by definition, narrowly distributed and therefore potentially sensitive to habitat destruction (e.g. Terborgh & Winter 1983). Second, political endemics highlight national responsibilities (Drinkrow & Cherry 1995).

The definition of 'endemism' can be problematic, and the term has been used to embody many concepts over the years. Originally the use of the term 'endemic' was ascribed to species confined to a set area under consideration in a particular study, typically a study area (e.g. Gelderblom & Bronner 1995), habitat type (Benson & Irwin 1966), or biogeographical entity (Crowe & Crowe 1982; Turpie & Crowe 1994; Muriuki *et al.* 1997). Such criteria are deemed 'biological' definitions of endemism. 'Political' definitions have also frequently been used, including political regions (Fanshawe & Bennun 1991), particular countries (Lombard 1995a), or political subdivisions within a country (Freitag & van Jaarsveld 1995). Muriuki *et al.* (1997) termed the former two concepts regional and national endemism for clarity.

Opinions vary on just how restricted a species' distribution must be to the area under consideration to qualify as 'endemic' to that area. Traditionally, a species had to be 100% restricted to an area to be considered an endemic (e.g. Williams *et al.* 1996b). However, cut-offs of 85% (Turpie & Crowe

1994) and 90 % (Lombard 1995a) have also been used. It has been argued that the use of such relative levels of endemism may well cause confusion, and so use of a 100% restrictedness criterion may be preferable (P.H.W. Williams pers. comm.). It can, however, be argued that the imposition of a 100% cut-off may result in somewhat artificial results. Biological knowledge is seldom complete. For example, the known distribution of a species may appear to be 100% restricted to an area of endemism, while the actual distribution of the species is slightly wider. It is seldom known precisely how complete our knowledge of a species distribution actually is. As a consequence, it can be argued that the absolute application of a 100% restrictedness criterion is overly zealous and implies a more complete knowledge than is often available. In addition, boundaries, even if biologically defined, are seldom discrete or absolute. Certain portions of the boundary may be weaker and less tightly defined (Williams 1996) than other portions. Species may well 'spill out' slightly of the area of endemism along such weak borders. These factors may well result in a number of species narrowly missing a 100% restrictedness definition of endemism. Although these arguments are valid, perhaps the traditional concept of endemism should remain as the 100% restrictedness definition, and the term of range-restrictedness (e.g. 90% range-restrictedness or 85% range-restrictedness) be used to express relative degrees of endemism.

These difficulties in pin-pointing a consistent definition of endemism are probably, in part, the reason why the concepts of endemism used in many studies have moved towards the definition of endemics simply as those species with very narrow distributions, rather than as species that are specifically restricted to a particular geographical area. Another reason why such range-size rarity definitions may be used instead of the concept of endemism is illustrated by the following example. Four species of small mammals that have ranges of less than 300 km^2 are not classified as endemic if the study area is defined as South Africa as their distributions fall across the political border between South Africa and Namibia (Gelderblom & Bronner 1995). The above example can be resolved by identifying species that have restricted range-sizes, irrespective of whether they are 'endemic' to some or other area. Consequently, among species globally restricted to subSaharan Africa (that is Afrotropical endemics), patterns of narrow distribution are investigated through measures of range-size rarity (narrow endemism *viz.* Williams *et al.* 1996b).

3.2. Methods

3.2.1 Measuring species richness and narrow endemism

In this study, species richness is calculated simply as a count of the number of species present in a grid cell. It is calculated for all seven of the species groups described in Chapter 2. The rare-quartile, a frequently used discontinuous measure of narrow endemism, gives greatest weight to the most restricted species (Gaston 1994). However, discontinuous definitions tend to be arbitrary and assemblages usually comprise species exhibiting a variety of range-sizes, which seldom separate into discrete groupings (Gaston 1994). Consequently, continuous measures of narrow endemism are often used, such as weighted richness by inverse range-size, termed range-size rarity (e.g. Csuti *et al.* 1997), which although dominated by rare species, considers all species (e.g. William *et al.* 1996b). This ensures that some components of diversity are not 'missed' because they narrowly fail to meet some set cut-off (e.g. Crowe & Brooke 1993; Crowe 1993). Narrow endemism is analysed by two separate indices of range-size in this study, namely the rare-quartile and range-size rarity.

Range-size rarity is not calculated for migrants or species not endemic to the Afrotropics as range-size calculations within the Afrotropics for such species would only constitute a portion of their total ranges. This could result in a widespread species that has a distribution that only marginally reaches into the Afrotropics being artificially identified as range-restricted.

3.2.2 Patterns and peaks of species richness and narrow endemism

Peaks in species richness and narrow endemism are highlighted by calculating hotspots for species richness and range-size rarity, defined as the highest scoring 5% of grid cells in the database for the measure being considered. The 5% criterion is an arbitrary, but frequently used, cut-off level (e.g. Myers 1988, 1990; Prendergast *et al.* 1993b; Lombard 1995a; Williams *et al.* 1996a). Patterns and hotspots of species richness and narrow endemism are investigated with WORLDMAP software (ver. 4.17.01, Williams 1997).

3.2.3. Comparison of overall patterns of species richness between species groups

The Spearman rank correlation was used to test for significant differences in distributional patterns of species richness between database subsets (e.g. Zar 1984). These correlations were calculated using STATISTICA software (release 5.1 A, for Windows, Statsoft, Tulsa, U.S.A.). Autocorrelation between grid cells *within* individual data bases exist, as all species barring single-cell endemics contribute to the species richness score of more than one grid cell within a data base. As a result, grid cells do not represent truly independent data points. The effect of this autocorrelation on the significance of results can be tested for by developing a frequency distribution of correlation values from randomly sampled subsets of grid cells within a particular data base. Frequency distributions are based on 1000 iterations. Coefficients and two-tailed probabilities derived from randomisation tests are displayed along side results for comparison of the full data bases.

3.2.4. Relations between centres of species richness and narrow endemism

It would be of interest to quantify the extent to which the occurrence of peaks in narrow endemism are dependent on the locality of peaks in species richness. This would help clarify the relation between species richness and narrow endemism. For instance, are peaks in species richness due to the presence of narrowly distributed specialists that facilitate niche packing? Is the coincidence of peaks in narrow endemism and species richness purely a result of mass effects – the more species present in an area, the greater the likelihood that at least some of these species will be narrowly distributed (e.g. Prendergast *et al.* 1993b; Gaston 1994)? Coincidence of a number of narrow endemics (indicating probable presence of neo-endemics and relicts) with peaks of species richness may well indicate centres of speciation (Crowe & Crowe's 1982 Type II refugia; Fjeldså *et al.*'s 1997 species pumps), although see Tuomisto and Ruokolainen (1997) for problems of using current distributional patterns to investigate historical events.

However, due to autocorrelation problems *between* data sets used to calculate species richness and narrow endemism scores for grid cells, statistics could not be used to gauge the extent to which centres of species richness and narrow endemics are related (interdependent). Autocorrelation in this instance results as the same species may contribute to both the species richness score and the narrow endemism score of a particular grid cell. These data sets also suffer from within data set

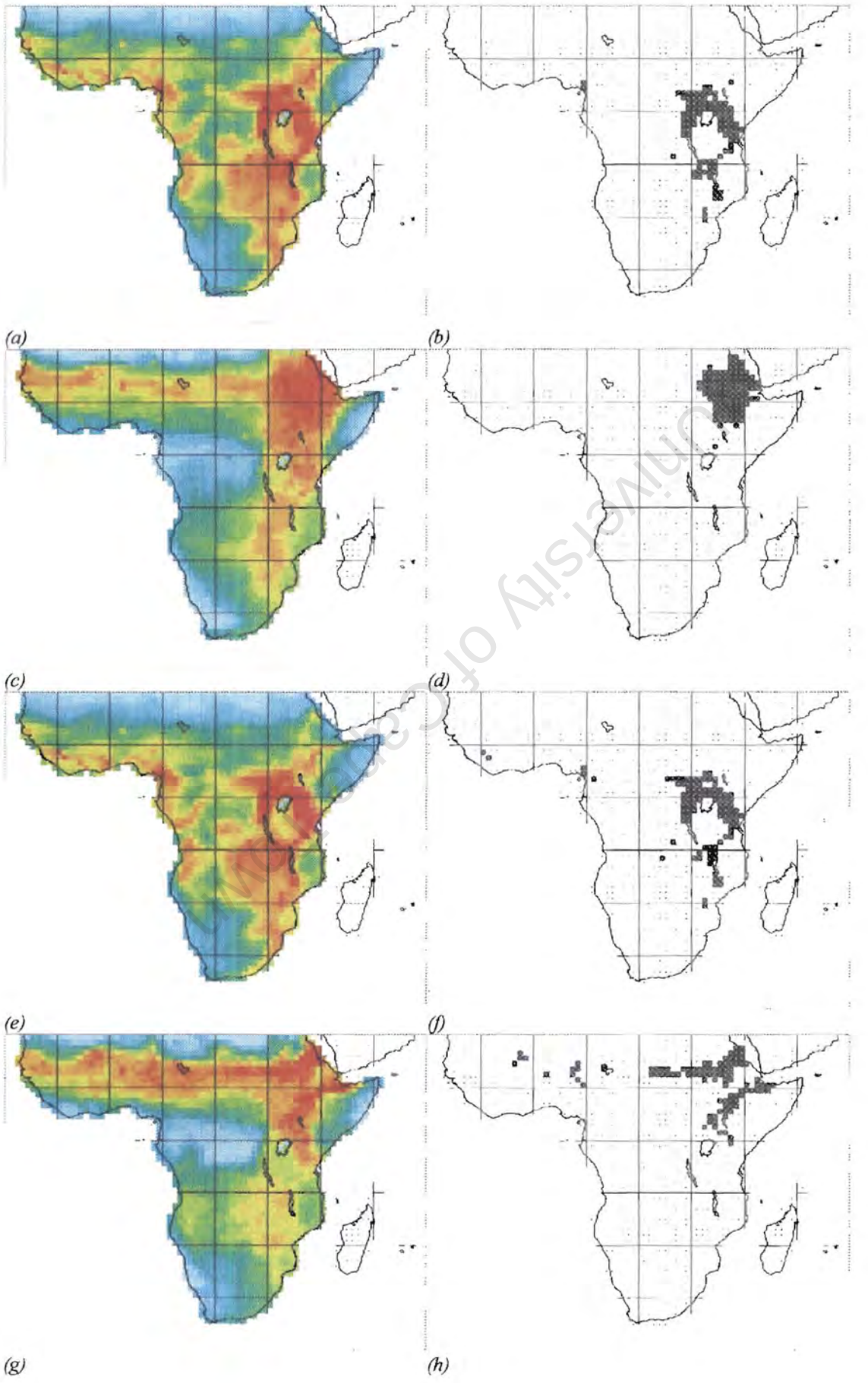
autocorrelation described in the preceding section. Consequently, simple visual comparisons of coincidence of hotspots of species richness and narrow endemism are made.

3.3. Results

3.3.1. Patterns of species richness

Patterns of species richness for all terrestrial species (including migrants) (Fig. 3.1a), breeding terrestrial species (including nonendemic species breeding in the Afrotropics) (Fig. 3.1e), and terrestrial Afrotropical endemics (Fig. 3.1i) are similar. The Ruwenzori mountains and adjacent Semliki lowlands occupy the grid cell that consistently scores highest (top hotspot), containing 469 of the 1646 Afrotropical endemics (32.66%) (Fig 3.1b). The Ruwenzori-Semliki grid cell falls within an area that generally shows a high species richness level stretching from the upper reaches of the Uelle River in the north of the Democratic Republic of Congo (formerly Zaïre), with one projection south along the Albertine Rift-Mitumba Chain west of Lake Victoria, and a second projection running around the north of Lake Victoria through Uganda, the mountains of southern Kenya and northern Tanzania and east of Lake Victoria along the Eastern Arc Mountains (as defined by Lovett 1988), south to the Nyika Plateau in northern Malawi. Other areas of high species richness include isolated mountains in West Africa (Loma, Nimba and Macenta), the Cameroon-Bameda Highland block and adjacent lowlands, the Angolan Escarpment, the *Brachystegia* woodlands of Zambia and Zimbabwe with particular peaks in the Katanga region in the southeast of the Democratic Republic of Congo (Mitumba Mountains/Lake Upemba area), the southern border area of the Democratic Republic of Congo and northeastern Zambia around Kalene Hill, the northern Muchinga Mountains, and Mt Milanje and Mt Chimanimani. Nonpasserine species endemic to the Afrotropics have hotspots in the Ethiopian Highlands not seen for passerines, while the latter highlight the Angolan Escarpment and Katanga.

The Ethiopian Highlands do not display high overall patterns (Figs. 3.1a, e & i) or peaks (Figs. 3.1b, f & j) in species richness, particularly if only Afrotropical endemics are considered. The minor peak seen when all terrestrial species are considered (Fig. 3.1a) is due to a high concentration of the of non-breeding migrants (Figs. 3.1c & d) and nonendemic residents (Figs. 3.1g & h).



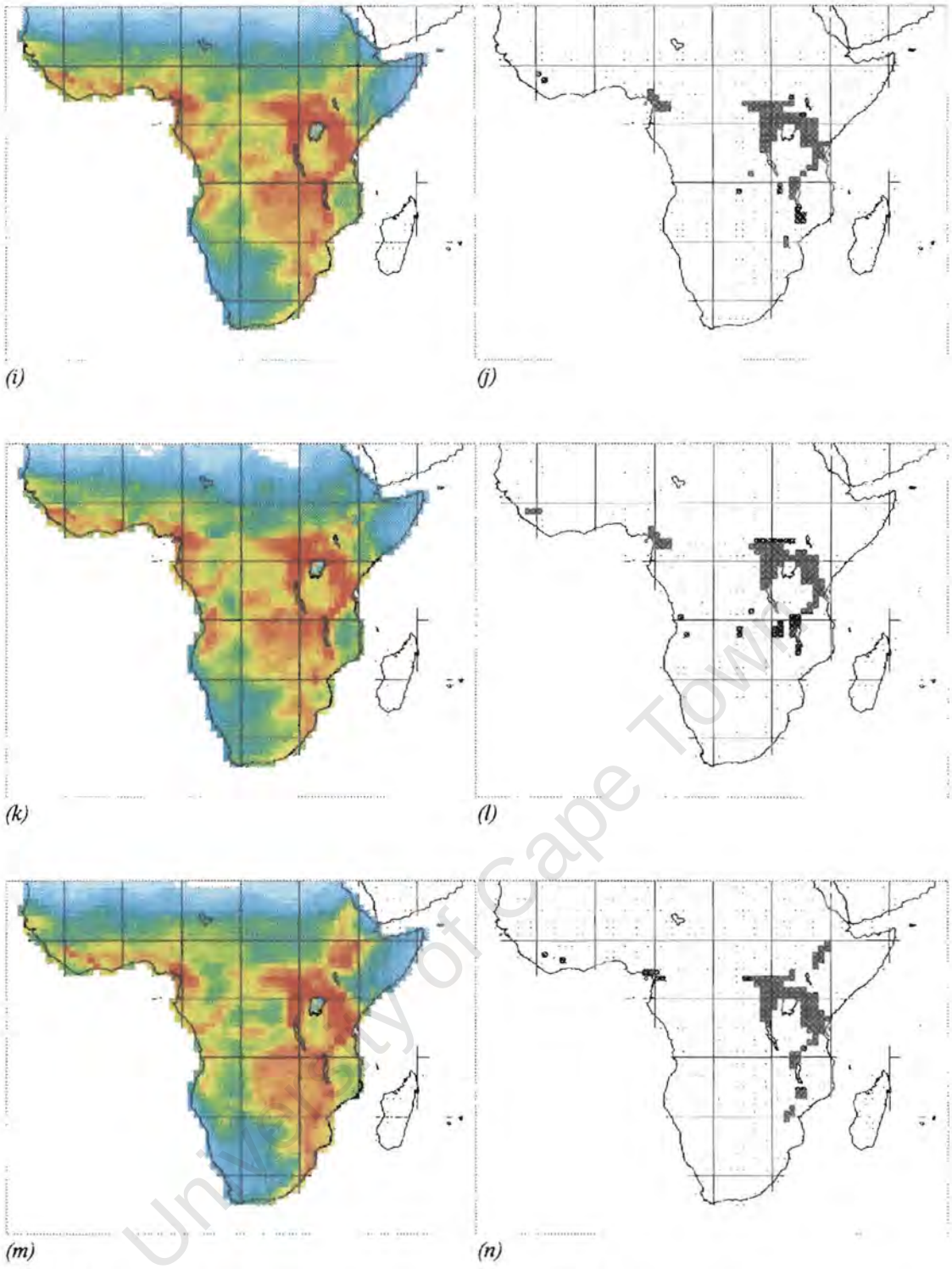


Figure 3.1. Patterns and hotspots of overall species richness for all terrestrial bird species occurring in the Afrotropics (a) & (b), terrestrial migrants to the Afrotropics (c) & (d), terrestrial residents in the Afrotropics (e) & (f), non-endemic residents (g) & (h), terrestrial Afrotropical endemics (i) & (j), passerine Afrotropical endemics (k) & (l) and non-passerine Afrotropical endemics (m) & (n).

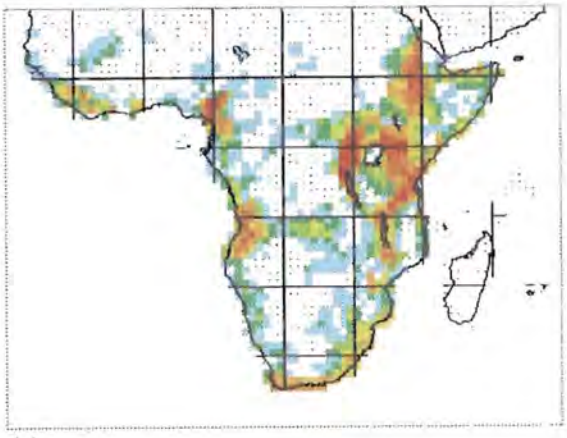
3.3.2. Patterns of narrow endemism

As with species richness, peaks of narrow endemism (as measured by both rare-quartile and range-size rarity) occur along the Albertine Rift and in the Kenyan, northern Tanzanian, Eastern Arc, and Cameroon-Bameda mountains and highlands, and the Angolan Escarpment (Figs. 3.2a-c, 3.3a-c, & 3.4a-c). The Fynbos and Highveld of South Africa score more highly under narrow endemism than they do under total species richness (Figs. 3.2a & b). Although some West African mountains are highlighted by species richness peaks, narrow endemism peaks accentuate these mountains more strongly, and identify additional mountains in this region. Nonpasserines endemic to the Afrotropics have a greater concentration of narrow endemics in the Ethiopian Highlands than do passerines (Figs. 3.3a-c). Passerines, in turn, highlight the Angolan Escarpment, Katanga region (in the southeast of the Democratic Republic of Congo), Mt Milanje (in northwestern Mozambique), the Chimanimani range (in eastern Zimbabwe), the Warsengalia hills (northern Somalia) and isolated localities along the Somali coast (Figs. 3.4a-c).

3.3.3. Comparisons of overall patterns of species richness between species groups

Spearman rank correlations between species richness patterns of subsets are displayed in Table 3.1. Endemic terrestrial passerines and nonpasserines are well correlated, although there is a preponderance of nonpasserines in the Ethiopian Highlands, Sudanian woodlands, and the eastern coastal vegetation mosaics of Zanzibar-Inhambane and Tongaland-Pondoland (Phytochoria nomenclature follows White 1983). Endemic terrestrial passerines are slightly more numerous than nonpasserines at the ends of the Arid Corridor (e.g. van Zinderen Bakker 1969) in the Somali-Masai bushland from Tanzania to Somalia and in the Kalahari and Karoo of South Africa and Botswana, as well as along the Angolan Escarpment and the Katanga region (southeastern Democratic Republic of Congo).

Patterns of species richness of endemics and nonendemic residents are significantly, but only very weakly, correlated (Table 3.1). High species richness values for both data sets are seen along the Rift Valley system and the mountains to the south thereof, extending to just north of the Drakensberg in South Africa (compare Figs. 3.1i & f with Figs. 3.1g & h). Slightly weaker coincidence of lower



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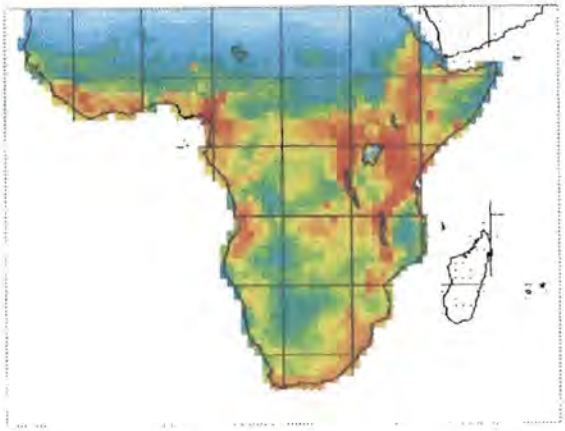

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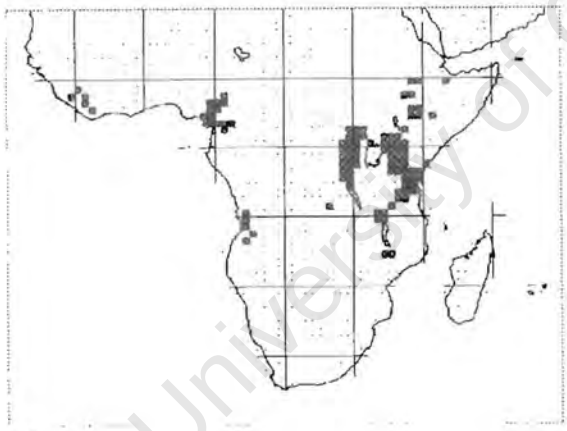
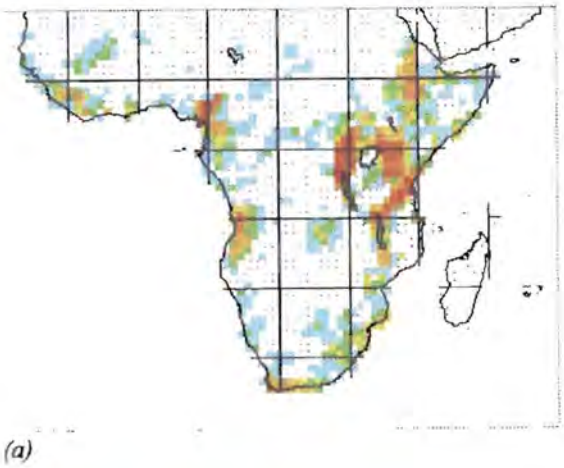


(c)

Figure 3.2. Patterns of species richness of rare-quartile species (the 25% of most range-restricted species) (a), patterns of range-size rarity (b), and 5% hotspots of range-size rarity (c) for all Afrotropical endemics.



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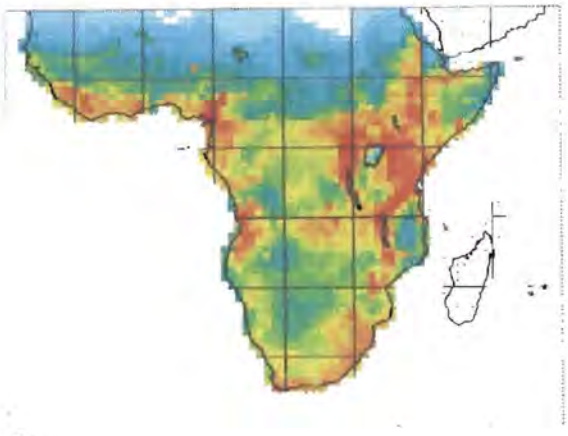

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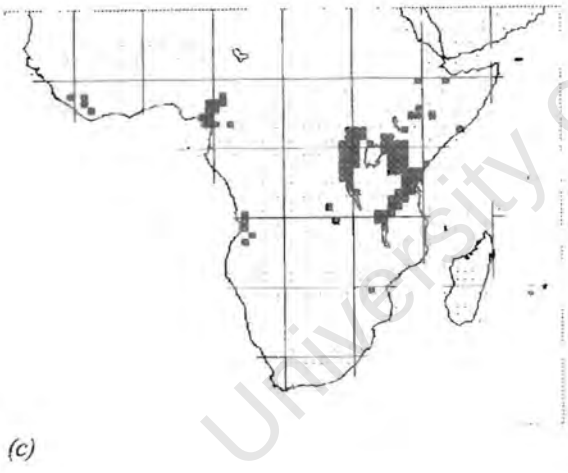
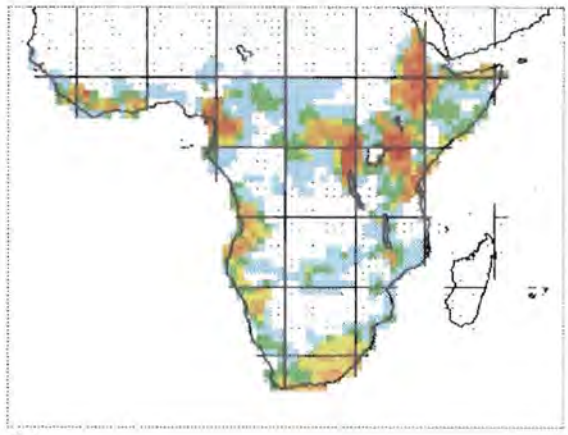
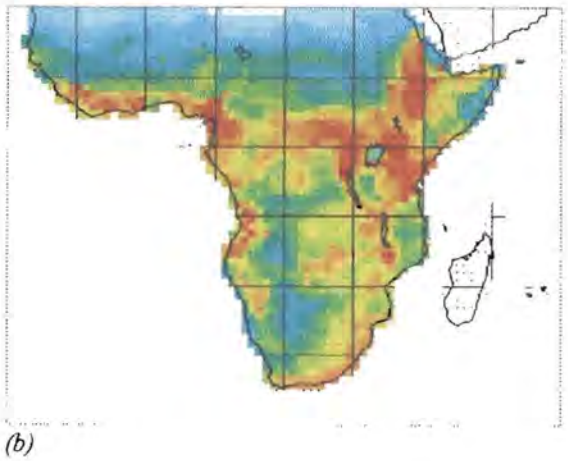


(c)

Figure 3.3. Patterns of species richness of rare-quartile species (the 25% of most range-restricted species) (a), patterns of range-size rarity (b), and 5% hotspots of range-size rarity (c) for passerine species endemics to the Afrotropics.



(a)



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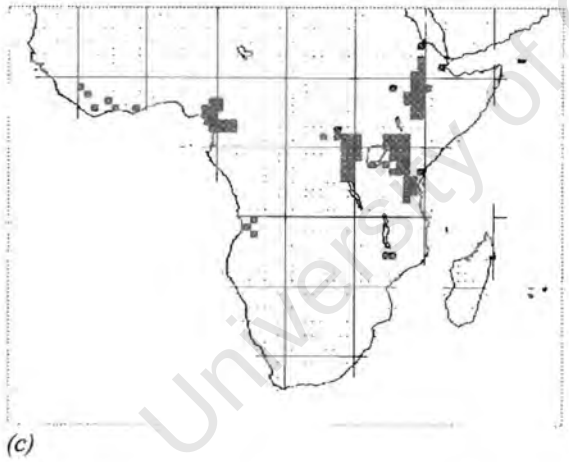


(c)

Figure 3.4. Patterns of species richness of rare-quartile species (the 25% of most range-restricted species) (a), patterns of range-size rarity (b), and 5% hotspots of range-size rarity (c) for non-passerine species endemics to the Afrotropics.

species richness peaks are seen along the West African forest-savanna transition and in the *Brachystegia* woodlands of Zambia, Malawi, and Zimbabwe. Nonendemic residents concentrate in the Sudanian woodlands and north of the Ethiopian Highlands into the Somali coastal hills (Warsengalia), whereas endemics predominate in the Guineo-Congolian forests and Highveld grasslands of southern Africa.

Terrestrial residents are significantly, but weakly, correlated with migrants (Table 3.1). Again there is a coincidence of grid cells that have high species richness scores for both data sets in and along the Rift Valley system and the mountains just south thereof, and along the West African forest-savanna transition (compare Figs. 3.1e & f with Figs. 3.1c & d). There is an apparent over-abundance of residents in the Guineo-Congolian forests, the eastern coastal vegetation mosaics of Zanzibar-Inhambane and Tongaland-Pondoland, Highveld grassland, and Drakensberg. Migrants concentrate in the Sudanian woodland belt that stretches across North Africa below the Sahel, with particular concentrations in the western foothills of the Ethiopian Highlands and the Ethiopian Rift Valley, and from there south into the arid regions of Kenya, and to the north and east (Haud) of the Ethiopian Highlands. A minor concentration of migrants in southern Africa is due to species that concentrate in the east of central and southern Africa (e.g. *Cuculus poliocephalus*, *Falco amurensis*, *Aquila pomaria*, *Locustella fluviatilis*, and *Hippolais olivetorum*) and the Kalahari (e.g. *Falco vespertinus*, *Lanius collurio*, and *L. minor*), and a migrant from Madagascar, *Cuculus rochii*.

Table 3.1. Correlations between species richness patterns of species groups exhibiting different distributional characteristics or life history strategies using the Spearman rank correlation. Results from randomised subsample tests (as described in the Methods) are presented in *italics* and bracketed.

Comparison	*Spearman rank rho*	*t (df)*	*Significance (2 tailed)*
Passerines vs. nonpasserines	0.909 (*0.922*)	96.690 (1959)	P << 0.01 (*P = 0.001*)
Endemics vs. nonendemic residents	0.157 (*0.221*)	7.015 (1959)	P << 0.01 (*P = 0.001*)
Residents vs. migrants	0.266 (*0.131*)	12.212 (1959)	P << 0.01 (*P = 0.001*)

3.3.4. Relations between peaks of species richness and narrow endemism

General patterns and peaks of species richness and narrow endemism visually appear to show quite high coincidence. However, important differences do occur. Peaks of narrow endemism not mirrored

by peaks of species richness occur in the Ethiopian Highlands (particularly for nonpasserines), Angolan Escarpment, Katanga Plateau, the Warsengalia hills (northern Somalia) and isolated localities along the Somali coast (particularly for passerines), and Cameroon lowlands. Additional species richness peaks not highlighted by measures of narrow endemism include the lowlands of the northeastern Congo basin (Ituri).

3.4. Discussion

3.4.1. Comparisons of overall patterns of species richness between species groups

Previous studies have suggested that nonpasserines and passerines show differences in general distributional patterns (e.g. Moreau 1966; Pomeroy & Ssekabiira 1990). It has been suggested that these differences are due to possible differences in selection pressures (Moreau 1966), with the diversity of passerines being due to a recent (Pleistocene) and currently active radiation (Moreau 1966; Pomeroy & Ssekabiira 1990). However, recent molecular studies are throwing this paradigm into question (J. Fjeldså pers. comm.). Although some differences are seen in overall patterns and peaks of species richness and narrow endemism in nonpasserines and passerines endemic to the Afrotropics, these are certainly not in the order suggested by the studies cited above (see also Crowe & Crowe 1982). Coincidence of patterns between these two species groups appears to be high, and may lend support (if somewhat anecdotal) for recent hypotheses emanating from molecular genetic studies regarding relative timing of peaks in speciation activity for nonpasserines and passerines.

Differences in species richness patterns between those species that have distributions centred outside of the Afrotropics (viz. nonendemic residents and non-breeding migrants) and those species that have distributions centred inside of the Afrotropics (Afrotropical endemics) can probably simply be attributed to island biogeography (MacArthur & Wilson 1967) and areography (Rapoport 1982) theory. These theories predict that highest species richness tallies will be found closest to the 'source'. Consequently, it is not surprising that numbers of species of nonendemic residents and non-breeding migrants are higher closer to the Palaearctic where they have their distributional centre.

Differences in species richness patterns between residents (endemics and nonendemics) and non-breeding migrants may indicate the role of life history strategy in determining distributional patterns. More detailed investigation of possible correlates and causes of these differences in species richness patterns are investigated in Chapter 4.

3.4.2. Relations between species richness and narrow endemism

Coincidence of hotspots of species richness and endemism has been shown to vary depending on taxa studied. For instance, Lombard (1995b) reports 5% coincidence for birds, 42 % coincidence for tortoises and 68% for snakes in South Africa. Gelderblom *et al.* (1995) showed coincidence to be low in Carnivora and Chiroptera, but high in Insectivora, the latter being less vagile, of smaller body size, and being greater habitat specialists. However, both these studies considered all species occurring in the study area, as opposed to just those species globally restricted to the study area. These studies are, therefore, affected by the marginal intrusion of species into the study area (known as the tropical subtraction syndrome), which boosts species richness in the north of the study area (namely South Africa). Hotspots of species endemic to the latter study area tend to be concentrated in the southwest, a geographically isolated area at the extreme of a continent (Gelderblom *et al.* 1995; Lombard 1995b). Thus, the low levels of coincidence of hotspots of species richness and endemism observed in these studies are perhaps not surprising. The same problem is encountered in two studies that compare species richness hotspots and narrow endemism in the British Isles (Prendergast *et al.* 1993b; Williams *et al.* 1996a). In these studies, species richness in both the south and the north of the British Isles is boosted by species whose distributions are centred in areas adjacent to the British Isles. Again it is not surprising then that hotspots of species richness, concentrated on the edges of the study area, and rare species do not coincide well.

In this study only those species whose global ranges are restricted to the Afrotropics (i.e. that are centred on the specific region under consideration) are included in analyses of coincidence of species richness and narrow endemism hotspots. Coincidence between hotspots of species richness and narrow endemism appears to be high. However, it must be emphasized that important mismatches occur. This together with the fairly large scale of the sampling units (one-degree grid cells), make it

difficult to outline any assumptions as to whether centres of species richness and speciation (i.e. narrow endemism) are coincident.

CHAPTER 4. Environmental correlates of species richness and narrow endemism patterns of Afrotropical bird species

Summary

Hypotheses put forward to explain patterns of bird species richness, narrow endemism, and distribution in the Afrotropics include elements of current environmental factors and ecology, as well as history. Current environmental variables purported to influence species richness include latitude, area (which could not be tested for in this study), rainfall, temperature, and vegetation diversity. Historical hypotheses are dominated by the notion of allopatric divergence in Pleistocene forest habitat refugia, although Fjeldså (e.g. 1994) suggests that localized climatic patterns of constant stability in a matrix that experiences periodic instability could have acted over shorter periods.

Hypotheses as to which extant environmental factors have influenced patterns, and approximations of the magnitude of their effect (what proportion of patterns they may explain), are fairly easy to test within statistical, hypothetico-deductive hypothesis testing protocols. However, it is almost impossible to test historical hypotheses within such a framework. As Tuomisto and Ruokolainen (1997) point out, testing of historical hypotheses is confounded by a paucity of relevant data and subjective interpretation of palaeoecological data, such that formulation and acceptance of historical hypotheses cannot be demonstrated within hypothetico-deductive testing frameworks.

Extant patterns, primarily of environmental stability (variability in rainfall, temperature ranges, and temperature extremes) and environmental harshness (average rainfall and absolute temperature ranges and temperature extremes) account for between 65.6 (migrants) and 79.5 (endemics) percent of variability in Afrotropical bird species richness. Mean altitude, altitudinal variability and a vegetation index (that encompasses both productivity and vegetation structural diversity) also play significant, but somewhat less important, roles. The significance of mean altitude and altitudinal variation in migrants and nonendemic residents is most likely due to the concentration of these species in the Ethiopian Highlands. Patterns of species richness in nonendemic residents and migrants are probably due to geography (as predicted by island biogeography and areography theory), with correlates of topography, and particularly temperature, probably being incidental. Vegetational structural diversity is probably more important than productivity in determining patterns of species richness (at the beta or gamma scale) of endemics.

Species richness patterns for the data sets of the different species groups (e.g. endemics vs. nonendemic residents, or all residents vs. non-breeding migrants) are correlated with similar sets of environmental variables. However, the different species groups place emphasis on different variables within the sets of environmental variables.

Topography and indicators of environmental stability (low variability in rainfall and temperature) are all significantly indicative of grid cells containing narrow endemics. No estimation of order of importance, or the magnitude of the effect of these variables on the occurrence of narrow endemics could be obtained from the non-parametric statistical analyses.

4.1. Introduction

This chapter is aimed at elucidating the role of the extant environment in determining patterns of Afrotropical bird species richness and narrow endemism on a broad scale. What environmental variables are correlated with these patterns, and what proportion of the variance in these patterns do they explain? Are the same environmental factors important for all bird species, regardless of their life history strategies? For instance, are the distributions of breeding residents and Palaearctic migrants affected by the same environmental factors?

Current biogeographical theory attributes patterns of faunal diversity (here species richness only with no measurement of abundance or evenness) to a combination of ecology and history (e.g. Mayr & O'Hara 1986; Ricklefs & Schluter 1993). Fine-scaled (alpha-level) ecological studies concentrate on competition, predation, and niche theory (see Ricklefs & Schluter 1993 for a review). Factors determining diversity on an intermediate scale (beta-level) include immigration and emigration, population dynamics, and turnover (e.g. Brown 1988). Broader, regional-scale (gamma- and delta-level) studies have often concentrated on area and latitude effects on diversity patterns (e.g. Pomeroy & Lewis 1987; Blackburn & Gaston 1996; Rahbek 1997). The scale of this study is too broad to explicitly consider the effects of competition, predation, immigration, and emigration. The latitudes spanned in the study region are narrow. In addition, the study of latitudinal effects on species richness patterns in the Afrotropics would be complicated by the fact that the number of grid cells per latitudinal band generally decreases south, and generally increases north, of the equator. Due to the fact that latitudes spanned in this study are narrow (relative to the scale of this study), the size of grid cells varies little over the study region. Consequently, possible diversity relations with area size and latitude are not investigated here. Productivity and environmental structuring (e.g. Brown 1988; Begon *et al.* 1990; Ricklefs & Schluter 1993) determine niche space and the diversity of niches available in a set area. Environmental productivity and structuring are, in turn, affected by temperature (available light and warmth), rainfall, vegetation structure, and altitudinal diversity (Brown 1988).

Causal factors promoting high levels of narrow endemism are attributed to environmental heterogeneity (e.g. Major 1988) and stability, both over shorter time-scales (e.g. Fjeldså *et al.* 1997) and over longer time-scales of the Pleistocene (e.g. Diamond & Hamilton 1980; Crowe & Crowe 1982; Fjeldså *et al.* 1997; H.P. Linder pers. comm.). A few studies suggest that long-term environmental stability in Africa is connected to current environmental stability (e.g. Fjeldså *et al.* 1997), which is determined primarily by predictability and evenness of rainfall. This study tests the predictive power of the magnitude and evenness of rainfall, temperature and productivity values, along with vegetation structural diversity and altitudinal diversity in determining patterns of species richness and of the presence of narrow endemics.

4.2. Methods

4.2.1. Species data

Six subsets of the 1646 terrestrial bird species that occur in subSaharan Africa were created to investigate whether differences in life history strategy (e.g. sedentary vs. migratory) and distributional characteristics (e.g. endemic vs. nonendemic) relate to differences in the significance of explanatory environmental variables. These species groups are outlined in Chapter 2, but are described here again for ease of reference. The seven resultant data sets are endemic terrestrial species (Afrotropical endemics: 1437 species), endemic terrestrial nonpasserine species (427 species), endemic terrestrial passerine species (1010 species), nonendemic terrestrial species that breed in the Afrotropics (nonendemic residents: 97 species), all terrestrial species which breed in the Afrotropics (1534 species), terrestrial non-breeding migrants to the Afrotropics (migrants: 112 species), and all terrestrial species (1646 species). Non-breeding migrants, chiefly from the Palaearctic, can be expected to display distributional patterns that differ from those of breeding residents due to differences in their life history strategies. Nonendemic residents are also expected to display distributional characteristics that differ from those of species that are wholly restricted to the Afrotropics, as the distributions of the former are not centred on the Afrotropics, whereas the distributions of the latter are. Although nonpasserines do not represent a monophyletic group, the endemic terrestrial data set was split into nonpasserines and passerines as the latter have possibly been subject to different selection pressures and possibly represent a recent explosive radiation (e.g. Moreau 1966, although recent molecular studies are throwing this paradigm into question, J. Fjeldså pers. comm.), and the two groups have been shown to have differences in general distributional patterns (Pomeroy & Ssekabiira 1990).

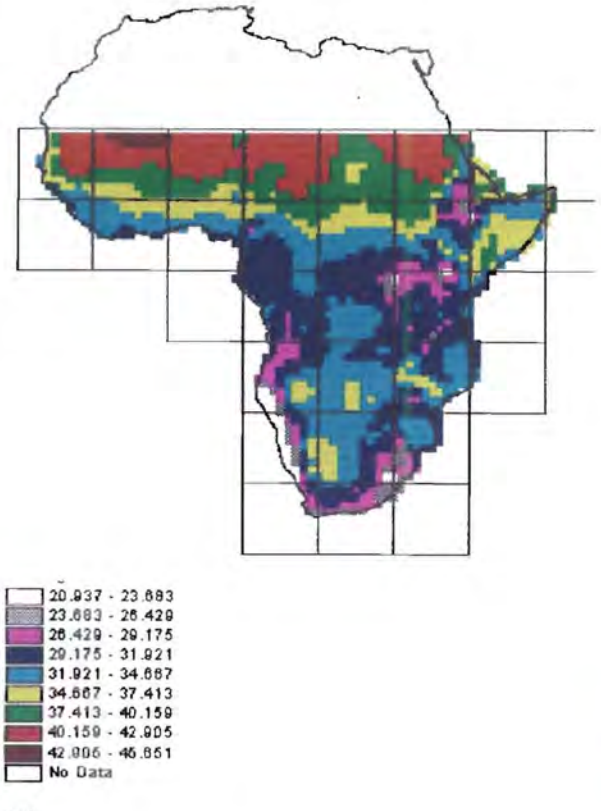
Species richness, as well as the presence and richness of narrow endemics, was calculated for each grid cell for each of the seven databases using WORLDMAP software ver. 4.17.01 (Williams 1997). Narrow endemics are defined for the purposes of this chapter as the rare-quartile (e.g. Gaston 1994; Williams *et al.* 1996a) so that grid cells can be categorized as 'containing narrow endemics (with narrow endemics)' or as 'not containing narrow endemics (without narrow endemics)'. If narrow endemism was defined here as range-size rarity, all grid cells would be categorized as containing narrow endemics, as range-size rarity is a continuous measure of narrow endemism (see also Chapter 3) and so considers all species.

4.2.2. Environmental data

4.2.2.1. Rainfall and temperature

Grid models at a 0.05 degree scale for mean monthly and total annual rainfall, and mean monthly and annual minimum and maximum temperatures, were obtained from the Centre for Resource and Environmental Studies (CRES), the Australian National University, topographic and climatic digital database (ver. 1.1). Each grid model is based on the data of over 1,500 weather stations gathered over a period of ca 60 years (Hutchinson *et al.* 1996). These data were generalized to a one-degree grid cell scale according to the mean, mode, median, and coefficient of variation of the 400 constituent values (some coastal grid cells are based on less than 400 values) using AGGREG (R. Navarro). Each of these methods of generalization was tested in a multiple regression to find the one that gave the strongest relation to richness in endemic terrestrial bird species. The median consistently gave the strongest R^2 values, and so all generalizations to a one-degree grid cell scale were based on median values.

The annual mean maximum (maxannT) and minimum temperatures (minannT) and the highest monthly maximum (maxmonT, Fig 4.1.a) and lowest monthly minimum (minmonT, Fig 4.1.b) temperatures attained for any one month, and the absolute temperature range (absTR, Fig 4.1.d), were used as estimates of the effects of temperature extremes. The mean annual temperature (meanannT, Fig 4.1.c) and mean monthly temperature (meanmonT) were also calculated. The variance (varmonT, varminmonT, varmaxmonT, varmonTR), standard deviation (sdmonT, sdminmonT, sdmaxmonT. sdmonTR), and coefficient of variation (cvmonT, cvminmonT, cvmaxmonT, cvmonTR) of the monthly mean, monthly minimum, monthly maximum and monthly range were used as estimates of the effect of seasonality, or variability, of temperature.



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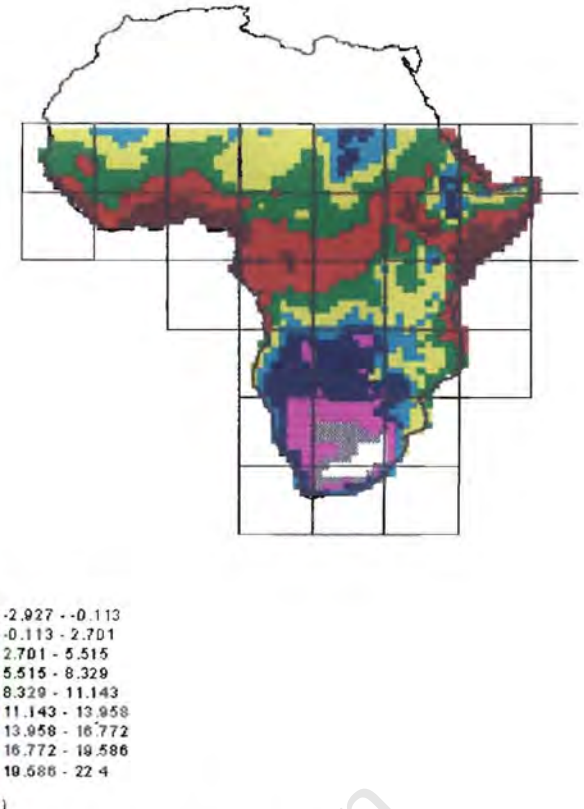

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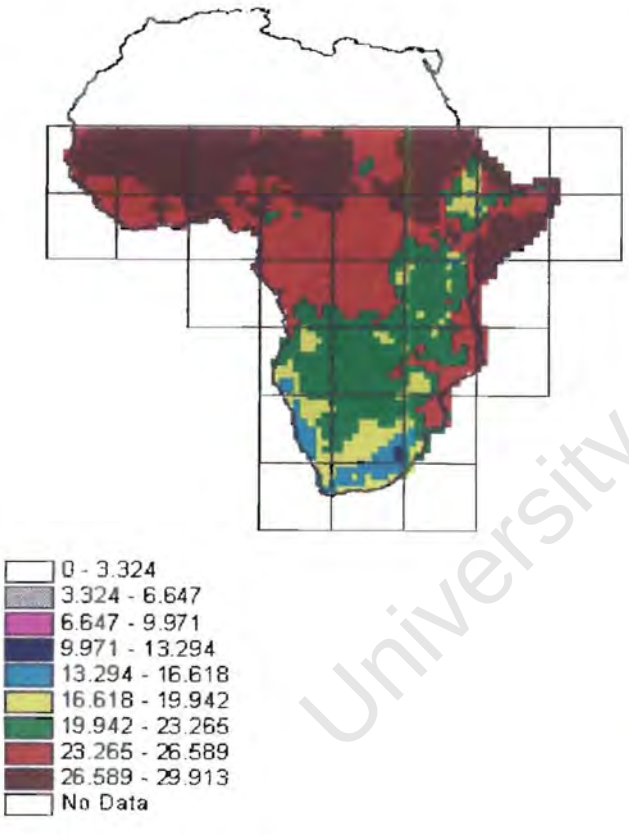

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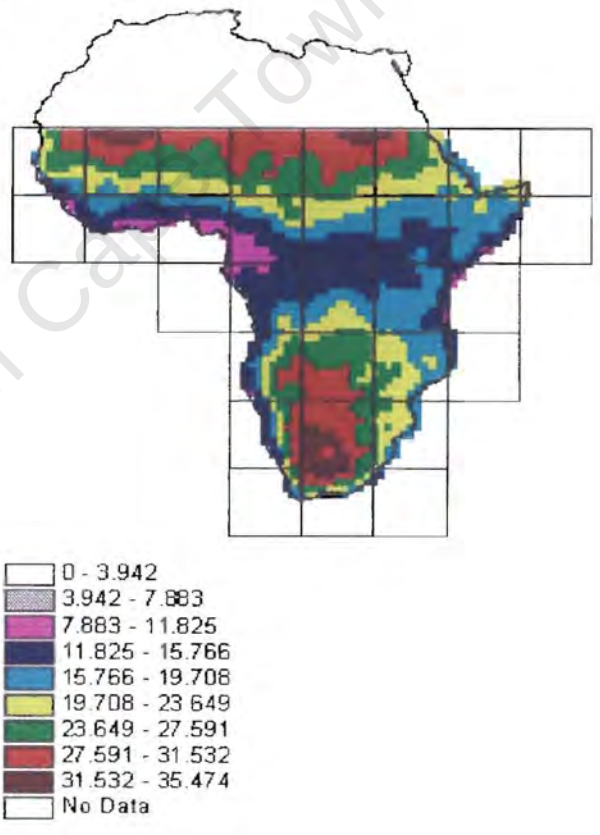

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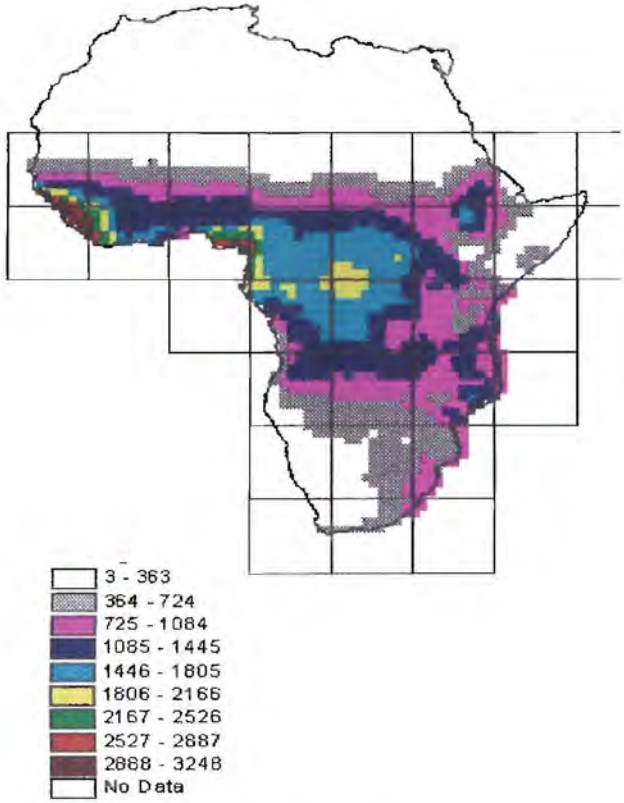

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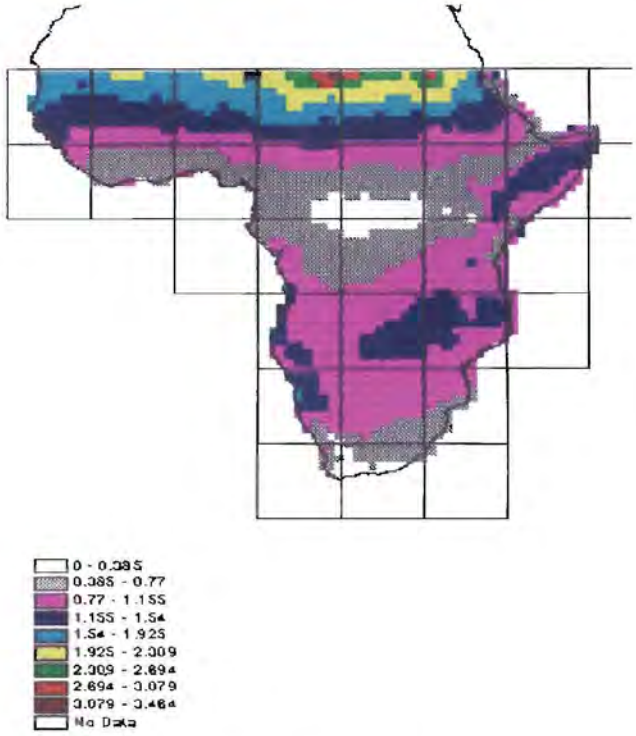

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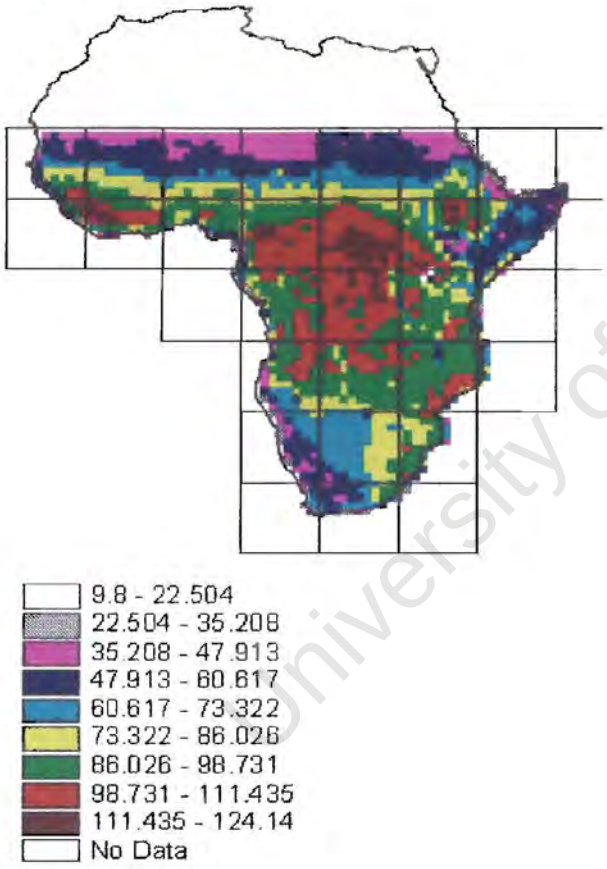

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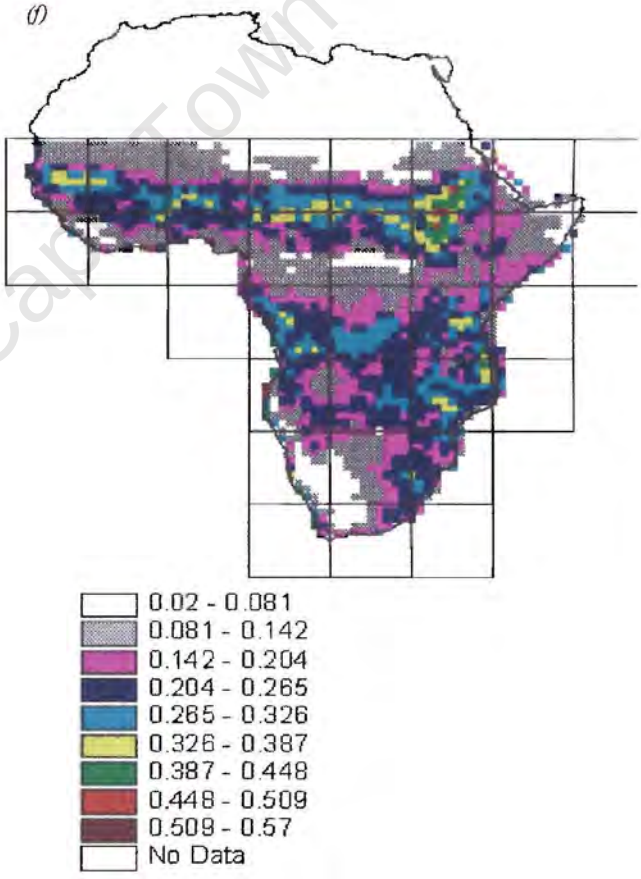

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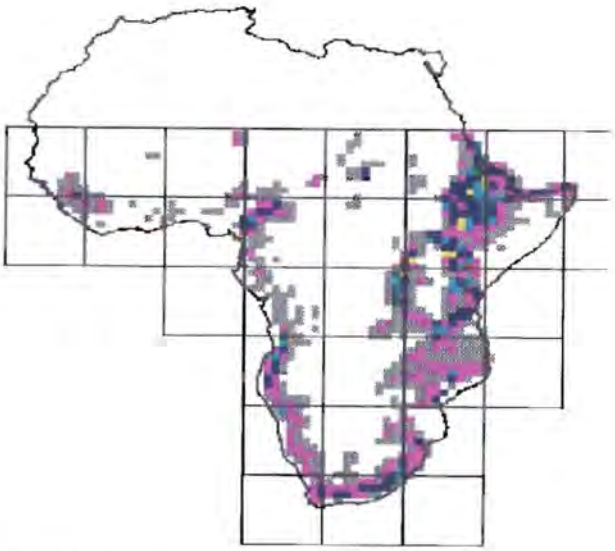

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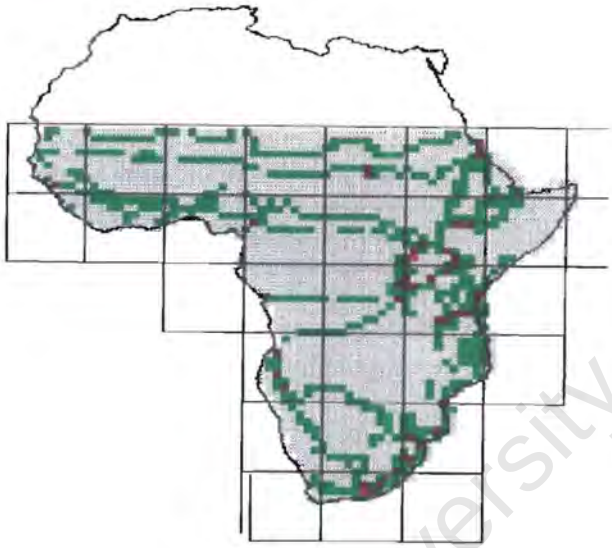

(j)

Figure 4.1. Data for (a) highest monthly maximum temperature (maxmonT), (b) lowest monthly minimum temperature (minmonT), (c) mean annual temperature (meanannT), (d), absolute temperature range (absTR) (e) total annual rainfall (totannR), (f) coefficient of variation of monthly rainfall (cvmonR), (g) mean monthly vegetation index (meanVI), (h) coefficient of variation in monthly vegetation index (cvVI), (i) altitudinal range (rangeA), and (j) number of major phytochoria (divveg).

The total annual amount (totannR, Fig 4.1.e), the mean monthly (meanmonR), and the maximum (maxmonR) and minimum (minmonR) values of rainfall attained for any one month were calculated as estimates of the effect of the amount of rainfall. The variability (varmonR), standard deviation (sdmonR), and coefficient of variation (cvmonR, Fig 4.1.f) of the monthly mean were calculated as measures of the effect of seasonality, or variability, of rainfall.

4.2.2.2. Altitude

A grid model of topography at a 0.05 degree scale was obtained from the CRES topographic and climatic digital database (ver. 1.1). ArcView (ver. 3, Environmental Systems Research Institute, Redlands, California) was used to obtain the total range (rangeA, Fig 4.1.i), mean (meanA), standard deviation (sdA), and coefficient of variation (cvA) of altitudinal values within each one-degree grid cell. Measures of variance of altitude within grid cells can be used to indicate the presence of topographically diverse terrain in a grid cell, rather than a single steep gradient or cliff which would not offer the range of habitats that a more gradual slope could potentially provide.

4.2.2.3. Diversity of vegetation types

Unfortunately, detailed digital information on vegetation diversity could not be obtained for the whole of the Afrotropical region. The best available surrogate was the number of major phythochoria (White 1983) occurring in each grid cell (divveg, Fig 4.1.j). To obtain these values, one degree grid cells were digitally superimposed using ArcView3 over a polygon coverage of the 15 phytochoria that occur on the Afrotropical mainland. However, due to the coarseness of this data, the maximum divveg value obtained for any grid cell was four, and most grid cells only obtained a score of one (average = 1.3 ± 0.515).

4.2.2.4. Vegetation Index

The monthly generalized vegetation index, which is a measure of productivity and vegetation structural diversity (Kinenman *et al.* 1992), was obtained from the Global Ecosystems Database ver. 1.0 (GED), (EPA Global Climate Research and NOAA/NGDC Global Change Database Programs). These data were collected at a 10-minute scale by NOAA satellites, and generalized to one-degree scale by the GED to provide the minimum, maximum, and mean monthly generalized vegetation index (minVI, maxVI, meanVI, see Fig 4.1.g for meanVI). The variance (varVI), standard deviation (sdVI), and coefficient of variation (cvVI, Fig 4.1.h) of the monthly mean over 12 months was calculated, using ArcView3, to provide estimates of the effect of seasonality, or variability, of productivity.

4.2.3. Analyses

4.2.3.1. Influence of environmental variables on species richness patterns

Generalised linear modelling was used to determine which of the independent variables were significantly related to the dependent variable, and the approximate order of importance of the variables. The assumption of normality in the data, as tested for using skewness and kurtosis (Tabachnick & Fidell 1989), was not met for a number of variables, but the data failed only marginally to meet the requirements. Recent studies show a range of parametric statistics to be more robust to violations of normality assumptions than was previously thought (Statsoft 1997:1417). In addition, normal plots of residuals of all regressions for species richness closely fit the expected-to-observed line (see Tabachnick & Fidell 1989 for discussion), so much so that it was decided to use generalised linear modelling for investigation of environmental correlates of species richness. Nevertheless, the fact that data are not normal, if only marginally not so, must be born in mind in interpreting results. For example, *based on these data*, it would not be valid to use residuals of regressions to infer refugia (*sensu* Crowe & Crowe 1982). Normal plots of residuals for richness in narrow endemics showed a considerably less tight fit than that seen in species richness analyses, such that a different approach was needed to elucidate the role of the environment in determining patterns of narrow endemism (see under the heading 'Environmental profile of grid cells containing narrow endemics').

4.2.3.2.Environmental profile of grid cells containing narrow endemics

Chi^2 tests were performed using STATISTICA software (ver. 5.1.H, StatSoft, Tulsa, U.S.A.) to determine environmental variable profiles for grid cells with and without narrow endemics. Environmental variables were classed according to quartile values. Chi^2 tests were used to determine whether observed frequency distributions of grid cells with and without narrow endemics across the quartile classes for a specific environmental variable differed significantly (e.g. Zar 1984). The significance of absolute adjusted residuals was calculated using RCTEST (R. Navarro; Everitt 1977). The results of RCTEST indicate which class(es) accounts for the significance of a result.

4.3. Results

4.3.1. Influence of environmental variables on species richness patterns

Variables describing environmental stability (*variability* in rainfall, temperature ranges, and temperature extremes) and environmental harshness (*average* rainfall and *absolute* temperature ranges and temperature extremes) are consistently the most important factors accounting for

variability in bird species richness patterns in all species groups analyzed, except migrants (Table 4.1). The latter group identified mean altitude as the primary explanatory variable, with environmental variability and harshness variables coming a close second. Mean altitude and altitudinal variability also play significant, but some what less important, roles for the other species groups, as does the vegetation index.

Environmental variables explain the greatest amount of the variation in species richness patterns for endemic terrestrial nonpasserines (R = 79.7) and the least for terrestrial migrants (R = 65.6).

Table 4.1. Results of generalised linear models showing overall model R-values (and std. error), and most important variables (derived from the t-values which are equal to the proportional relation between the size of the estimate and the std. error; see for example Moore & McCabe 1993). See Appendix 4.1 for full listing of estimates of regression coefficients for all variables within a model.

Life History Group	*R (std. error)*	*Variables*
All Endemic spp.	79.5 (38.5)	cvmonR$^-$, sdminmonT$^-$, and maxVI$^+$ (measures variability in monthly rainfall$^-$ and temperature$^-$, maxmonT$^-$, and absTR$^-$)
Endemic passerine spp.	77.5 (25.4)	cvmonTR$^+$ and cvmonR$^-$ (maxVI$^+$, minVI$^+$, and absTR$^-$)
Endemic nonpasserine spp.	79.7 (14.9)	cvmonR$^+$ and varmonR$^+$ (sdmonT$^+$, sdmonTR$^+$, and cvA$^+$)
Nonendemic residents spp.	72.7 (6.24)	totannR$^-$, cvmonR$^-$, maxmonT$^+$, and meanA$^+$ (sdminmonT$^+$ and varminmonT$^-$)
All breeding residents	78.0 (41.5)	cvmonR$^-$, cvmaxmonT$^-$, and sdmonT$^+$ (absTR$^-$, sdminmonT$^-$, and totannR$^+$)
Non-breeding migrant spp.	65.6 (7.61)	sdmonT$^+$, minmonT$^+$, and sdmonTR$^+$ (sdmonR$^-$ and sdmaxmonT$^-$)

4.3.2. Environmental profile of grid cells containing narrow endemics

Frequencies of grid cells containing narrow endemics are significantly *lower* than expected in areas with highly seasonal rainfall, very high temperatures, and high temperature ranges (Table 4.2). Frequencies of grid cells containing narrow endemics are significantly *higher* than expected in areas with higher altitudinal ranges, variability of altitude, and meanVI, although these relations are of smaller magnitude than those with rainfall and temperature (Table 4.2). Strength, or magnitude, of relations are inferred from the size of the difference between the 'observed minus expected' frequency to the observed frequency. Large differences are taken to indicate strong relations. Significance of absolute adjusted residuals indicate that the variable classes 1 and 4 (i.e. the extremes) almost always account for the significance of results.

Table 4.2. Chi² test of significant differences between grid cells with and without narrow endemics (df = 3, p<0.01 for all cases). The classes accounting for the significance, as indicated by significance of absolute residuals, are presented.

Variable	*Chi²*	*Strength of relation*
TotannR	116.258	Less than expected for very low levels of totannR
CvmonR	265.033	Less than expected at high levels cvmonR
MaxannT	463.688	Less than expected at medium and very low levels maxannT; greater than expected at medium and very high levels maxannT. Classes 1 & 4 show larger observed-expected values than classes 2 & 3
MaxmonT	514.279	Less than expected at medium and very low levels maxmonT; greater than expected at medium and very high levels maxmonT. Classes 1 & 4 show larger observed-expected values than classes 2 & 3
MinannT	121.634	Less than expected at medium and very low levels minannT; greater than expected at medium and very high levels minannT. Classes 1 & 4 show larger observed-expected values than classes 2 & 3
MinmonT	32.560	Less than expected at medium high levels of minmonT; greater than expected at very high levels of minmonT
MeanmonT	301.867	Greater than expected at medium and very low levels of meanmonT; less than expected at very high levels meanmonT. Classes 1 & 4 show larger observed-expected values than class 2
CvmonT	117.036	Greater than expected at very low levels cvmonT; less than expected at very high levels of cvmonT
AbsTR	326.429	Greater than expected at medium and very low levels of absTR; less than expected at very high levels absTR. Classes 1 & 4 show larger observed-expected values than class 2
RangeA	362.943	Less than expected at medium and very low levels rangeA; greater than expected at medium and very high levels rangeA. Classes 1 & 4 show larger observed-expected values than classes 2 & 3
CvA	224.652	Less than expected at very low levels of cvA; greater than expected at very high levels of cvA
MeanVI	88.525	Lower than expected at medium and very low levels meanVI; higher than expected at medium and very high levels meanVI
CvVI	43.580	Lower than expected at very low levels cvVI; greater than expected at medium high levels cvVI

4.4. Discussion

4.4.1. Relations between species richness patterns and environmental variables

Previous studies have shown that temperature and rainfall variables are significantly related to bird species richness at regional and landscape scales (e.g. Crowe & Crowe 1982: the Afrotropics; Braithwaite *et al.* 1989: *Eucalyptus* forests of Australia). These variables may act directly on individual species, as shown in local-scale studies (e.g. Parker 1996; Lloyd & Palmer 1998). These results could be explained in terms of physiological limits of birds as follows. Birds, as with other endothermic animals, need to maintain body temperature within a particular range [39-40 for nonpasserines and 40-41 for passerines: see Schmidt-Nielsen (1990) and references therein as for the rest of this paragraph] in order to ensure proper functioning of physiological process and to prevent degradation of proteins and cellular structures. Individuals can maintain these body temperatures over a range of ambient temperatures through physiological (e.g. evaporation) and behavioural (e.g. huddling as seen in Emperor Penguins, *Aptenodytes forsteri*) mechanisms. Simple mechanisms such as 'gular flutter' to aid heat loss through evaporation may be common to many bird species and

enable a large number of bird species to survive a certain range of ambient temperatures. However, in areas where temperatures range in excess of those which 'regular' mechanisms can deal with, special adaptations are required, such as reductions of thermal windows through a thick down covering in Pteroclidae (Maclean 1985). Accordingly, distributions of species without specialised adaptations may be expected to be curtailed, and levels of species richness in such areas can be expected to decline. Similarly, availability of water, both in terms of predictability and abundance might have direct bearing on the survival of individuals and their ability to breed. Adaptations to very arid climates include highly efficient cloacal water resorption in Pteroclidae (Thomas & Maclean 1981), ability of kidneys to eliminate excess salts, producing smaller amounts of urine and of higher salt concentration as seen in the Ostrich, *Struthio camelus*, production of very dry faeces in Starke's Lark, *Eremalauda* (ex *Alauda*) *starki*, and Grey-Backed Sparrow-Lark, *Eremopterix verticalis*, and an ability to tolerate higher osmotic pressures e.g. Savannah Sparrow, *Passercullus sandwichensis* (Maclean 1974). Salt secreting glands found in many marine species to deal with saline or hypertonic water or body fluids of prey animals are also found in arid adapted plovers, *Charadrii,* and Gabar Goshawk *Micronisus gabar* (Maclean 1984). Belly wetting of specialised feathers provides a means of cooling eggs in shorebirds, especially plovers (Maclean 1983) and carrying water to chicks at the nest (e.g. Maclean 1984). Some species eat succulent vegetation, e.g. the Ostrich (Louw 1972 cited Maclean 1974).

The effect of rainfall and temperature probably also acts through vegetation as suggested by Moreau (for temperature, 1935) and Chapin (for rainfall, 1932), particularly at the broad regional scale of this study. This relation is supported by the high correlation between rainfall and temperature variables and the vegetation index ($r_{totannR} = 0.83$, $r_{cvmonR} = -0.66$, $r_{maxmonT} = -0.54$ and $r_{sdmonT} = -0.65$; see also Brown 1988). The vegetation index (VI) is derived from the differences in spectral reflectance of channel 1 (visible band) and 2 (infrared band) measurements of NOAA Polar Orbiting Environmental Satellites (Kinenman *et al.* 1992). This difference indicates the presence of green vegetation and is affected by leaf, plant, and canopy structure (Kinenman *et al.* 1992). Thus, the VI indicates both the productivity (amount of green biomass) and structural complexity of the vegetation (Kinenman *et al.* 1992). Consequently, it is difficult to ascertain whether the significant, positive relation between meanVI and species richness (for all data sets) is due to productivity or structural diversity, both of which are touted as explanatory variables of species richness (see Brown 1988; Begon *et al.* 1990; Ricklefs & Schluter 1993 for detailed discussion). Productivity is thought to increase the number of species present in an area rather than simply the size of populations of existing species. Physical structural complexity of vegetation is thought to facilitate coexistence of species directly through niche differentiation, which leads to a reduction in competition and an increase in

predator-safe refuges. Brown (1988) suggests a tight relationship between productivity and structural complexity. Birds require certain structures as part of their environment, such as perches, breeding sites, and shelters from predation (Brown 1988). Such structures are more abundant in more productive environments, so that productivity affects species richness both directly though the provision of more resources, and indirectly and specifically through vegetation structural complexity (Brown 1988).

While it may be true at an *alpha* diversity level that productivity is strongly related to both vegetation structural complexity and bird species richness, productivity probably has less of a direct influence at a *beta* or *gamma* diversity level, such as the scale used in this study. Rather, correlation between the meanVI and species richness at an Afrotropical scale probably indicates a general increase in species richness from structurally simple, single vertical layer habitats such as grasslands, through two-layered habitats of savannas and woodlands, to multi-layered rainforests (H.P. Linder pers. comm.). This is supported by Estades (1997) who found that species richness, Shannon-diversity, and density of birds in the central Chilean Andes was significantly correlated with foliage height diversity (a measure of structural complexity) when all sites along a habitat gradient from grasslands to temperature forest were included. When either non-forest sites or forest sites alone were considered, foliage height diversity was no longer related to bird species richness. Estades' results indicate that actual foliage height diversity *within* a vegetation type is probably not as important a factor in determining species richness as differences in structural diversity and complexity *between* vegetation types.

The role of mean altitude and altitudinal range in explaining variability in non-breeding migrant species richness is largely due to the concentration of migrants in the Ethiopian Highlands and along the Rift Valley system. The grid cells falling within the Ethiopian Highlands and along the Rift Valley system have large ranges in altitude (Fig. 4.1i). The Rift Valley system represents a major flyway (Fanshawe & Bennun 1991; Pearson & Lack 1992) and a wintering ground (Pearson & Lack 1992) for a number Palaearctic migrants. Rapoport (1982) suggests that migrants are forced to pass through East Africa as they circumvent the Guineo-Congolian forests, which represent a dispersal barrier to these species (e.g. Fry 1992; Leisler 1992). Note that the situation in the Neotropics, where migrants make considerable use of forest habitats, is quite different (e.g. Keast 1980 and references therein). The relation of altitude with species richness may also be due to the increase in land area in grid cells that contain mountains, resulting in simple species-area relationships (MacArthur & Wilson 1967). Identification of vegetation diversity by both these groups could be due to the fact that eastern

Africa in the vicinity of the Rift system represents a complex 'habitat melting pot' (Chapin 1932; Moreau 1966; Pomeroy & Lewis 1987).

High species richness values of nonendemic residents and terrestrial migrants occur in the northern and northeastern parts of the Afrotropics. These areas are occupied by desert or semi-arid vegetation in the form of the Sahara, and particularly the adjacent Sahel, and the Horn of Africa. This explains the relation between species richness of these two data sets with environmental variables characteristic of desert and semi-desert habitats, such as temperature extremes (minmonT, maxmonT, absTR) and seasonality (e.g. cvmonT, cvmonR). The importance of maxmonT values in particular is due to the richness of migrants in the Sudanian woodland belt, which experiences maxmonT values of around 40°C, a figure that is only exceeded in the Sahel (Fig. 4.1a). It is this richness of migrants and nonendemic residents in the Sudanian woodland that results in species richness patterns of these two data sets being so weakly correlated with those of Afrotropics endemics (see Figs. 3.1c & g in Chapter 3). The concentration of migrants in the northerly reaches of the Afrotropics, and subsequent decreases in the species richness of these groups with distance from the northern 'boundary' of the Afrotropics, could be due to geographical or biological factors. Island biogeography (MacArthur & Wilson 1967) and areography (Rapoport 1982) theory suggest a drop-off in faunal resemblance with distance from the point of origin (i.e. Eurasia in most instances, although see Leisler 1992 for discussion of the possible origin of some migrants in the Afrotropics). Decrease in species richness of migrants with distance from their breeding grounds is noted for both the Afrotropics (Fry 1992; Leisler 1992 and references therein) and the Neotropics (Keast 1980 and references therein).

A possible biological factor resulting in the concentration of migrants in the north of the Afrotropics could involve their exclusion by residents in habitats south of the Sudanian woodland and Horn of Africa. Moreau (1966, 1972) suggests that seasonal lows of resources in the northern savannas preclude an abundance of resident species being supported the year around. Indeed, the Sudanian woodland experiences the greatest seasonality in productivity (Fig. 4.1h), which results in the importance of variability in the vegetation index in explaining the patterns of species richness of migrants. The comparatively smaller seasonality experienced in the southern savannas could be postulated to result in higher abundances of residents. Residents have been shown in both the Afrotropics (Leisler 1992) and Neotropics (Keast 1980 and references therein) to be competitively dominant to migrants. The possibly greater abundance (or rather species diversity) of competitively dominant residents could be suggested to preclude migrants from entering areas in the southern savannas in the same numbers as they do in the northern summers (this argument is presented in the Neotropical literature, see Keast 1980). However, one direct problem with this line of argument is

that there may be no need for many of the migrants to travel further than the northern savannas to overwinter. Recent work (see Leisler 1992 for discussion of relevant studies) shows that resources may not decrease in as spectacular a fashion during the stay of the migrants in the northern savannas as previously thought (c.f. Moreau's 1972 paradox, see for example Fry 1992). The productive systems of the Niger inundation zone, Lake Chad, and the Sudd provide sustained food availability during the migrants' stay (see Leisler 1992 for discussion). If indeed resources are not lower in the northern savannas than in the southern savannas during the period of the migrants' stay, there may well be no impetus to migrate further south.

Environmental variables explain more than three quarters of the variability in species richness patterns of endemic terrestrial species. They explain just less than three quarters of the variability in species richness patterns of nonendemic residents, and two thirds of the variability in species richness patterns of terrestrial migrants. The lower powers of explanation of the model for the patterns of species richness of migrants could be taken to indicate that additional factors not considered in the model, such as competitive exclusion by residents, are involved in determining these patterns. However, such results could also be predicted from island biogeography and areography theory. Lower numbers of species in the migrants and nonendemic residents data sets could also result in weaker statistical relations between patterns of species richness of these two species groups and environmental variables. In addition, the uneven patterns of species richness of migrants over the face of subSaharan Africa results in these data being more skewed than that of some of the other species groups, such as Afrotropical endemics. Consequently, it is difficult to know how much information can be derived from the magnitude of these correlation analyses.

Although current carrying capacity (productivity, vegetation structural diversity and altitudinal habitat diversity) appears to play a role in determining patterns of species richness in Afrotropical birds, the main emphasis of results was on environmental stability and harshness. Environmental harshness may well impose physiological constraints (as discussed above). However, stability is probably more important. The mechanisms through which stability affects species patterns are likely to be varied and complex. For instance, current stability may well allow species packing (Begon *et al.* 1990). Current inter-annual variability may well be linked to historical variability (see Fjeldså *et al.* 1997 for a discussion on this relation). An example of the possibility of such a relation may be seen in the greater stability (and productivity) of the northeastern and northwestern portions of the Congo basin, which are identified in a number of studies as refugia (Diamond & Hamilton 1980; Crowe & Crowe 1982), as compared with the lower stability (as well as productivity and habitat diversity) of the central basin, which observation is confirmed by Louette (1984). Consequently it is tenable that

currently stable areas may well have been stable over the medium (Fjeldså 1994; Fjeldså *et al.* 1997) or long (Haffer 1969, 1997; Diamond & Hamilton 1980; Crowe & Crowe 1982) term.

4.4.2. Environmental profile of grid cells containing narrow endemics

Chi^2 analyses emphasise the importance of stable and moderate climates in determining the presence of narrow endemics. Productivity seems to be somewhat less important than stability in determining the presence of narrow endemics. The significant, positive relation between range and variability in altitude indicates the role of mountainous regions in determining the presence of narrow endemics. Mountains provide increased habitat diversity through vertical zonation of vegetation along mountain slopes, and provide a wide range of microclimatic sites (Gelderblom & Bronner 1995). These factors may be expected to increase the number of species occurring in a limited geographical area and the number of niches available for specialization. However, it must be noted that apparent sympatry of species in grid cells with high altitudinal range scores may not translate to true sympatry on the ground. Species which are vertically allopatric or parapatric will appear sympatric within a flat database that cannot depict vertical structuring (e.g. Prendini 1995; Gelderblom & Bronner 1995). At the scale of this study, altitude probably acts by increasing vertical zonation and vertical allopatry of species within grid cells, rather than through increasing microclimatic sites and hence niche volume. However, it must be noted that the occurrence of narrow endemics in areas that are locally stable and topographically diverse, indicates a complex interaction between these factors. J. Fjeldså (pers. comm.) emphasises the fact that narrow endemism is often correlated with local ecoclimatic stability which exists due to orographic moderation of climatic extremes within topographically complex areas.

It is postulated that mountains often maintain localized climatically stable patches (Sprugel 1991; Coe & Skinner 1993; Fjeldså & Lovett 1997; H.P. Linder pers. comm.), such that the effect of environmental stability and altitudinal variation may not act completely independently, but may rather be partially linked. Stability is likely to promote both persistence of relicts and speciation of new forms. This connection of richness in narrow endemics and stability is strengthened by the significant negative relation between temperature extremes and seasonality with richness in narrow endemics in nonpasserine terrestrial Afrotropical endemics and all terrestrial Afrotropical endemics.

Areas containing narrow endemics that do not coincide with mountains occur in Katanga (southeast Congo basin), along the east African coast, and along the Congo and Niger Rivers. This may reflect the influence that the sea and larger rivers have been reported to have on local climatic fluctuations

(e.g. Hamilton 1982). Katanga constitutes a moderately high plateau dissected by deep river gorges, which results in high levels of plant endemism and replacement (H.P. Linder pers. comm.). In addition, there is also much 'replacement' of plateau grassland, forest extending along the river gorges, and *Brachystegia* woodland (e.g. Lynes 1938) creating a rich habitat mosaic on the Katanga Plateau.

4.5. Conclusions

As suggested by many authors, currently observed patterns of bird distribution in the Afrotropics are probably due to a combination of ecology and history (e.g. Diamond & Hamilton 1980; Crowe & Crowe 1982; Mayr & O'Hara 1986). However, it is difficult to determine the relative magnitude of the effects of current environmental and historical factors on these patterns. For instance, generalised linear models show that the current environment probably explains between 65.6 (for migrants) to 79.5 (for endemics) percent of variability of species richness of terrestrial birds in the Afrotropics. But these analyses cannot determine whether the residual is due to poor data (e.g. skewed data) or history. In addition, these analyses cannot determine whether the size of environment correlation has been driven by the current environment, or whether it was driven by historical factors that happen to coincide with the current environmental correlates. For instance, Chi^2 analyses showed that occurrence of narrow endemics is correlated with environmental stability and altitudinal complexity. These factors are likely to act through determining current environmental carrying capacity and they probably indicate a causal link to historical factors. Localized environments currently experiencing environmental stability are probably situated in such a way that these areas have also been stable over the medium to long term (Coe & Skinner 1993; Fjeldså *et al.* 1997; H.P. Linder pers. comm.).

Generalised linear models can indicate the most important environmental correlates, but they cannot indicate whether or not such correlates are causative. For instance, environmental stability and harshness are most important in determining species richness patterns for endemics, while mean altitude also plays a strong role in determining species richness patterns of nonendemic residents and migrants. Vegetation structural complexity and productivity have been shown to influence bird species richness directly at small scale studies (e.g. Estades 1997). However, the correlations for nonendemic residents and migrants cannot be assumed to be causal as their distributional patterns could well be determined by simple island biogeography and areography theory (namely concentration of species closest to their point of origin) and avoidance of 'unsuitable' habitat (Rapoport 1982). Exclusion of migrants by residents is possible, but less strongly indicated in the literature for the Afrotropics as compared to the Neotropics.

CHAPTER 5. Biogeographical patterns of endemic terrestrial Afrotropical birds

Summary

Cluster and characteristic species analysis identify 36 areas of distinct and homogeneous avifaunal composition. These 36 avifaunal zones fall within six subregions, namely the Northeastern, Northern Savanna, Southern Savanna, Guineo-Congolian, Southwestern and Northern Arid Subregions. The number of zones per subregion varies from two in the Northern Arid Subregion to 10 in the Southern Savanna Subregion. Results were well corroborated by turnover analysis of biogeographical zonal boundaries and by a literature review.

Probable roles of historical features such as refugia (or locally stable patches within unstable matrices c.f. Fjeldså 1994; Fjeldså et al. 1997), physical barriers and corridors, may well be supported in patterns of distribution of Afrotropical birds. However, it is often difficult to discern the possible relative importance and effects of history and the current environment, as statistical analysis cannot differentiate between history and current patterns of redistribution (e.g. Fjeldså & Lovett 1997; Haffer 1997; Tuomisto & Ruokalainen 1997).

5.1. Introduction

The study of patterns of distribution of African bird species has a long history in Africa, ranging from the descriptive studies of Chapin (1923, 1932) and Moreau (1966), to the use of multivariate techniques by Crowe and co-workers (Crowe & Crowe 1982; Guillet & Crowe 1985) and Diamond and co-workers (Diamond & Hamilton 1980; Diamond 1985). More recently Fjeldså and co-workers (Fjeldså 1993, 1994; Fjeldså & Lovett 1997; Fjeldså *et al.* 1997) have used genetic distance based on the DNA/DNA hybridization data of Sibley and Ahlquist (1990) to assess approximate ages of species, and have related these to historical and ecological processes, speciation, and refugia models. The Crowe, Diamond, and

Fjeldså studies all used distributional data from the Atlases of Speciation of African Birds (Hall & Moreau 1970; Snow 1978). The intervening two decades have seen considerable improvement in knowledge of both the taxonomy and distribution of birds in subSaharan Africa. This paper aims to revisit the field of Afrotropical avifaunal biogeography through the use of a database created through extensive literature searches on published distributional information, and a combination of analytical techniques. The database was compiled jointly by the Percy FitzPatrick Institute and the Danish Centre for Tropical Biodiversity. The resulting database is both more up to date and finer-scaled than those used in previous studies.

Biogeographical entities can be identified by distinguishing geographical regions holding distinct and homogenous avifaunas in the Afrotropics (*sensu* Chapin 1923:123), that is 'zone centres', or by recognizing regions of transition between one avifauna and a neighbouring avifauna, that is zonal boundaries. Regions of distinct and homogenous avifaunas are typically distinguished through the use of multivariate techniques of agglomerative (Crowe & Crowe 1982; Guillet & Crowe 1985) or divisive (Diamond & Hamilton 1980; Williams *et al.* in press) clustering algorithms and ordination (Williams *et al.* in press). This study follows a similar approach to that of Crowe and co-workers (Crowe & Crowe 1982; Guillet & Crowe 1985) through the use of an agglomerative clustering algorithm (to avoid the recognition of artificial zones in the data that may arise from rules of set number of divisions and group size of divisive algorithms, see Diamond & Hamilton 1980). Biological validity of groupings identified by the agglomerative algorithm are verified by 'characteristic species' analysis (Crowe & Crowe 1982; Guillet & Crowe 1985) and by comparisons of mutlivariate analysis results with previous studies both at the continental (Chapin 1932; Crowe & Crowe 1982) and subregional (e.g. Benson & Irwin 1966; Winterbottom 1978; Diamond & Hamilton 1980) levels, and by publications reflecting detailed field knowledge and studies (e.g. Lynes 1938; Louette 1984). Transitional regions were originally identified as areas showing high levels of turnover (beta-diversity *sensu* Whittaker 1960). Whittaker (1960) described turnover as the change in community composition between sample plots along an environmental gradient. Some authors (Wilson & Shmida 1984; Harrison *et al.* 1992; Williams 1996)

specify that turnover must only measure species replacement with no overlap (see Williams 1996 for measurements of turnover that are sensitive to varying amounts of overlap in biotas within transitions). Although a few authors argue that species richness trends also constitute a valid part of turnover (C. Rahbek pers. comm.) this study considers only species replacement as indicative of turnover. Williams (1996) and Williams *et al.* (in press) developed indices that measure both aspects, that is absolute replacement and species richness trends, separately. Such indices can provide information as to whether a biogeographical boundary is due to the replacement of one avifauna by a different neighbouring avifauna, or whether the biogeographical boundary is only due to the loss of species, or 'species drop-outs', representing the transition between one avifauna and a neighbouring, relatively depauparate subset of that avifauna.

The use of a number of approaches to describing biogeographical regions and the correspondence of analytical results to studies based on field knowledge reduces the chance of recognising artificial avifaunal zones. It also provides information on factors which may have created and maintain these patterns of distribution.

5.2. Methods

5.2.1. The database

Although all of the 1646 terrestrial species occurring in the Afrotropics will have played a part in shaping the avifaunas of the region, migrants and nonendemic species are mostly cosmopolitan, having wide distributional ranges, and are thus biogeographically uninformative. In addition, this study was not able to split transit, stop-over and wintering-site records for migrants (see also Chapter 2), such that migrant records are coarsely plotted as having ranges much larger than their wintering-sites. Due to these reasons, data for migrant and nonendemic species will probably mask or confound the identification of fine-scale partitioning of avifaunas. Consequently, the cluster analysis used herein is based on terrestrial Afrotropical endemics (n = 1437). Although nonpasserines do not form a monophyletic group,

nonpasserine (n = 427) and passerine (n = 1010) species are analysed as two subsets of the Afrotropical endemics, to investigate possible differences in general distributional patterns between the two groups (Moreau 1966; Pomeroy & Ssekabiira 1990). However, the assertion that passerines as have possibly been subject to different selection pressures and possibly represent a recent explosive radiation (e.g. Moreau 1966) have been recently contested by findings of molecular studies (J. Fjeldså pers. comm.).

5.2.2. Patterns of distribution

5.2.2.1. Distance index and cluster algorithm

The Bray-Curtis distance index is used as a measure of dissimilarity (1 minus the similarity) to compare each grid cell to every other grid cell based on its species composition (e.g. Everitt 1993). The Bray-Curtis measure is used as it does not consider conjoint absences (Sneath & Sokal 1973; Krebs 1989), which would have been inappropriate in this study as data are based on presence only information and does not include confirmed absence information. A hierarchical classification algorithm is applied to the resultant distance matrix in order to indicate groupings, or clusters, of grid cells that comprise similar avifaunas, and to indicate how these clusters relate to each other (Gauch 1982). Choice of algorithm is largely determined by the type of input data (Cunningham & Ogilvie 1972 in Everitt 1993). Hands and Everitt (1987) found that for binary data, with clusters of different sizes, centroid algorithms performed best. Hence an UPGMC (unweighted pair-group method using centroid) (Sneath & Sokal 1973:234) algorithm was applied. BMDP-2M software (Dixon 1990) was used to implement both the Bray-Curtis distance measure and the UPGMC classification algorithm.

5.2.2.2. Cluster validity – cluster size, number of clusters, similarity value

The decision as to which of the clusters identified by the classification algorithm constitute valid biogeographical entities can be reached in a number of ways. One approach is to define 'stopping rules', such as 'minimum group size' and 'maximum level of divisions' (Hill 1994). Minimum group size of a cluster can be specified such that a cluster of the specified size will not actively be subdivided further (although smaller groups may be caused by the natural structure of the data, see Hill 1994:32).

Maximum level of divisions specifies the number of groups to be formed (Hill 1994:33). These stopping rules have been applied to divisive algorithms, but the philosophy could also be applied to dendrograms generated by agglomerative methods. Another stopping rule is a 'set level of distance or similarity'. There are, however, no objective guidelines as to what minimum group size, maximum level of divisions, or particular distance or similarity level might be appropriate in any particular study, or what the effect of varying the values of the stopping rule may be. In addition, in a study region that shows great variation in species richness, such constant cut-off approaches may not be valid if the relationship between variation in species richness and these various cut-off approaches is not understood. For instance, the number of species present in an area may be expected to affect the strength of the distance or similarity relationships between grid cells by determining the size of the available species pool from which such relations may be drawn.

5.2.2.3. CLUSTER VALIDITY – CHARACTERISTIC SPECIES AND DISTINCT AVIFAUNAS

Everitt (1993:2) maintains that as any classification scheme simply represents a division of objects into groups based on a set of rules, such that a classification is neither true nor false and so should be judged on the usefulness of the results Our purpose is to *identify geographical regions of distinct and homogenous avifaunas in the Afrotropics based on their complement of bird species*. In many instances, such avifaunal regions might be expected to be characterised by unique species. A characteristic species is defined (*sensu* Crowe & Crowe 1982) as one that has a distribution that is both largely restricted to, and coincident with, the boundaries of a particular geographical area (avifaunal zone). A species may be restricted to an avifaunal zone, but its distribution may not help to delineate the boundaries of that zone. Such species are termed zone-restricted (c.f. Crowe & Crowe' 1982 endemic species). Characteristic species are, therefore, by definition, a subset of zone-restricted species (see Table 5.1 for congruent concepts used in other studies). The presence of a few zone-restricted species, and particularly characteristic species, will corroborate that a cluster of grid cells (an avifaunal zone) identified by the cluster analysis is a valid biological entity. However, a geographical area may have a combination of bird species that differs to the combinations of bird species found in adjacent areas despite a lack of unique

species (characteristic or zone-restricted species) in the area under consideration. Such an area may represent a distinct avifaunal zone, according to the aim outlined above. The validity of clusters of grid cells identified by the algorithm that fall into this category is harder to test. In such instances, studies published on these areas and their constituent avifauna have been consulted.

Table 5.1. Definitions used in a number of published studies to identify species that support the identification of biogeographical zones.

This study:	Zone-restricted species	Characteristic species	Zone-associated species
Crowe & Crowe (1982):	Endemic species	Characteristic species	
Braun-Blanquet's floristic association method (as used by Westhoff & van der Maarel 1973):	Local character species	General (exclusive and selective) character species	Preferential species
Hill (1994):		Differential or indicator species	
Clarke & Warwick (1994):		Discriminating or Typical species	
Turpie & Crowe (1994):	Endemic species	Characteristic species	
Muriuki *et al.* (1997)	Endemic species	Characteristic species	

The application of this methodology also necessitates the use of arbitrarily defined cut-off levels. A percentage cut-off at which a species is classified as zone-restricted or characteristic must be decided on. There are no hard and fast rules that can be applied to the definition of an appropriate cut-off level. Approaches vary from the 100% restrictedness in classic definitions of narrow endemism (Williams *et al.* 1996a), to the 50% cut-off of the Braun-Blanquet floristic association method as used by Westhoff and van der Maarel (1973). This study investigated how the number of zone-restricted and characteristic species was affected when the percentage cut-offs were varied at 5% intervals from 60% to 100%. This study also investigated the relationship between the number of zone-restricted and characteristic species

per percentage cut-off, with zone size and zonal species richness, as well as how the number of characteristic species changes with the number of zone-restricted species defined. Large variation in the species richness of grid cell both within and between subregions confound patterns. In addition, there are a few small zones with particularly high species richness (e.g. the Albertine Rift and Eastern Arc Provinces) and one or two very large zones with particularly low richness (e.g. the Northern Arid Province) that mask any relationship that there might be between zone size and zonal richness, such that no clear trends could be identified.

It can be argued that any species that has *more* than 50% of its range confined to a zone is more strongly affiliated with that zone than with any other zone, which reasoning is congruent with that of the Braun-Blanquet approach (Westhoff & van der Maarel 1973). This approach was used to define zone-associated species considered in analysis of conservation priorities (see Chapter 6). However, such a low cut-off is too broad to be useful in identifying species that support the recognition of particular avifaunal zones. The number of zone-restricted species identified for all zones dropped off sharply as the percentage cut-off was increased from 60 to 65 and from 65 to 70, whereafter it decreased more slowly. Consequently, the arbitrary cut-off of 70% was decided on. It would possibly be inappropriate to use a very high cut-off level on data of this scale (each grid cell represents ca 110 x 110 km) and accuracy. There are a number of biases which may cause species to appear artificially widespread. Firstly, baseline are often derived from range maps which, no matter how conservatively interpolated from point data, may still result in errors of commission (that is, species being represented as present where they do not occur) (e.g. Gelderblom & Bronner 1995). Secondly, digitizing range data into a grid system will lead to inaccuracies when a very narrowly distributed species' range evenly straddles a line of latitude or longitude. Such a species would then be included as present in both grid cells either side of the line of latitude or longitude, such that the species' range will appear relatively broader in the digital database than it is on the ground. An attempt to correct for this bias was made by plotting very restricted species from verified point records only. Due to these problems with the database, it would be inappropriate to use, for instance, a 100% cut-off criterion since the potential exists for a number of species, which may in

fact meet such a criterion on the ground, to fail to meet it in the analysis due to biases in the digital data. For the same reason, it is not appropriate to implement a cut-off in an absolute fashion. For example, *Tockus jacksoni* is 67.9% restricted to the Lake Turkana district, but has been considered as a zone-restricted species as its extra-zonal records all fall immediately adjacent to the zone and in the same habitat type to which the majority of its records are restricted (see also Crowe & Crowe 1982). This approach may seem to be inconsistent, but cognisance must be taken of what this study is trying to portray by the identification of zone-restricted species, that is to highlight species which are primarily associated or affiliated with a particular zone. As the 70% cut-off is in any case an arbitrary one, it seems sensible to not use this criterion blindly, but to be guided by the distributions of the individual species.

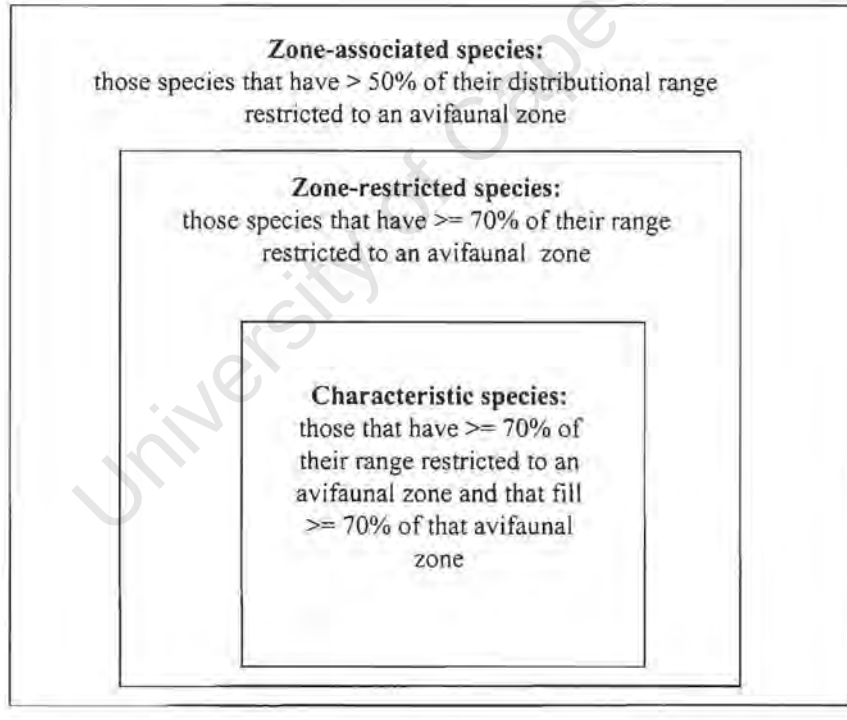

Figure 5.1. Distributional species concepts used in this study to aid identification of avifaunal zones.

For a cluster of grid cells to be accepted as valid avifaunal zone, it had to contain at least one characteristic species, or be supported by published avifaunal studies on the area under consideration (for

example, Benson & Irwin 1966 support the recognition of an Angolan Highland avifauna despite the lack of characteristic species). All calculations to determine zone-restricted and characteristic species were performed using GIS - ARC/INFO (ver. 6.1.I., Environmental Systems Research Institute, Redlands, California).

5.2.2.4. CLUSTER NOMENCLATURE

Major divisions of the dendrogram are termed subregions. Subregions are broken down into avifaunal provinces. In some instances, clear structure occurs within provinces depicting distinct avifaunas that are supported by characteristic species or published literature. Such avifaunal structures are termed districts. Usage of the terms district, province, and subregion loosely follows Crowe and Crowe (1982:419). However, whereas Crowe and Crowe's (1982) usage of these terms corresponded specifically to clusters identified by subspecies, species, and genera respectively, no such taxonomic approach to area classification is inferred by the use of these terms in this study. 'Zone' is used as a generic term for any cluster of grid cells, whether it be a district, province, or subregion.

5.2.2.5. TURNOVER AND RANGE-EDGES

Species replacement is measured as neighbourhood (comparison of the grid cell under consideration with its eight closest neighbouring grid cells, i.e. its first- and second-order neighbours; see Williams 1996 for further description) segregation. Segregation aims to measure complete spatial replacement with no overlap, based on Rapoport's segregation index (1982; see Williams *et al.* in press for details). Species richness gradients are measured as neighbourhood heterogeneity, that is the sum-of-squares of deviations from the mean richness within the neighbourhood (see Williams *et al.* in press for details).

5.3. Results

Six subregions are identified by the cluster analysis for terrestrial birds endemic to the Afrotropical mainland (Fig. 5.2a for all Afrotropical endemics; Fig. 5.3a for endemic passerines; Fig. 5.4a for endemic

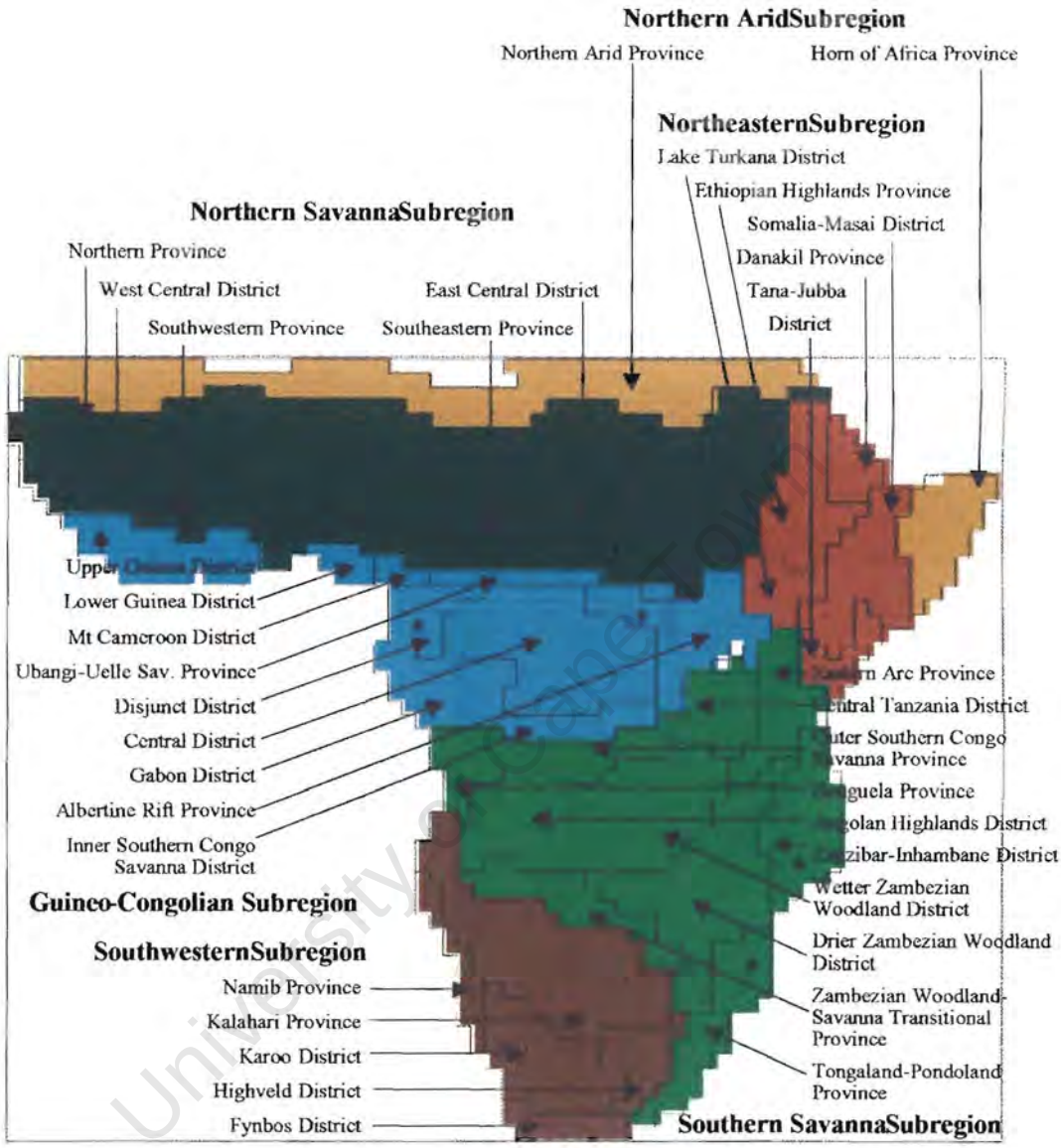

Figure 5.2.a. Patterns of distribution as defined by cluster analysis terrestrial endemic Afrotropical bird species

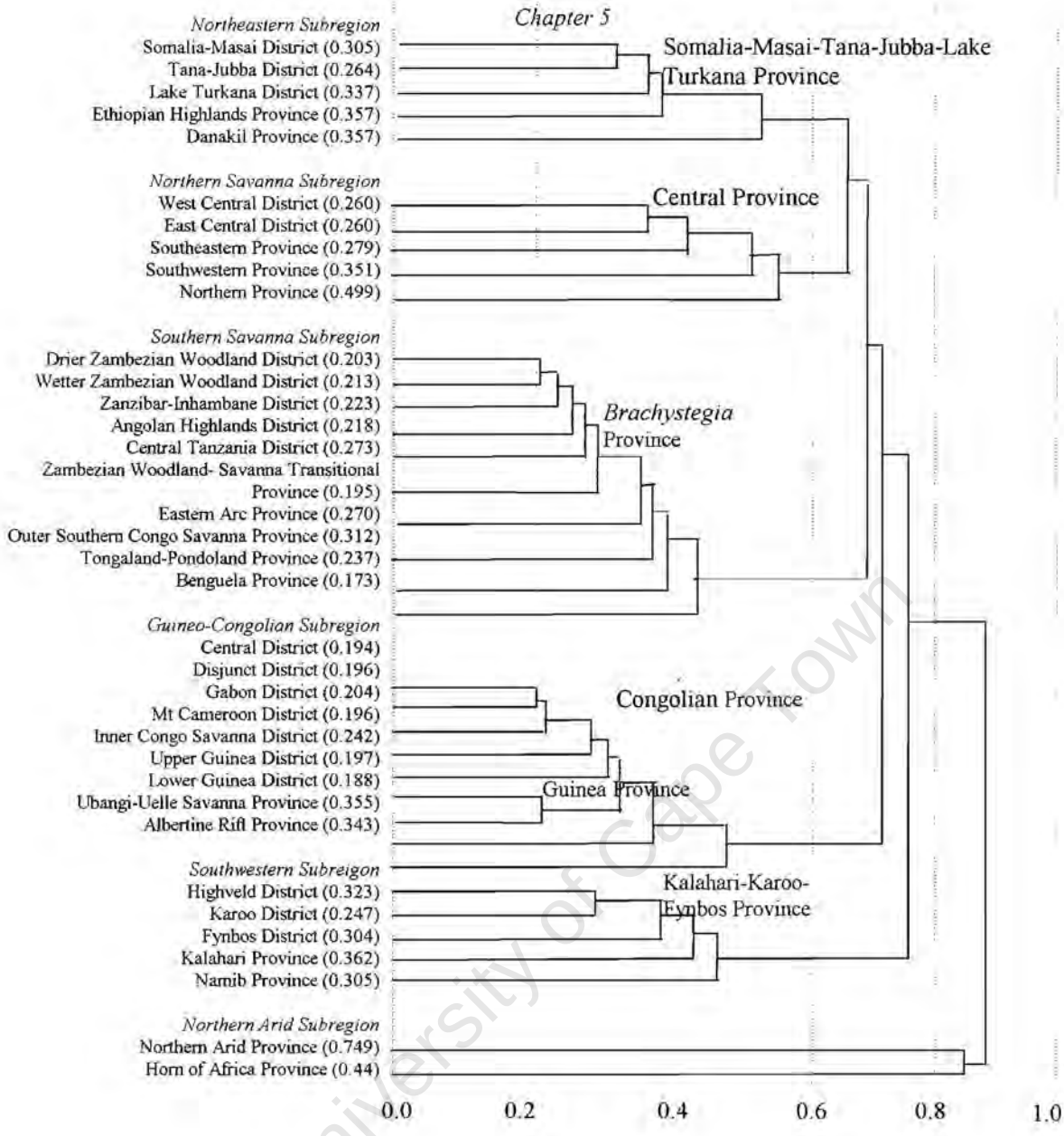

Figure 5.2.b. Relations of avifaunal zones defined by a cluster analysis on presence data for 1437 terrestrial endemic Afrotropical bird species.

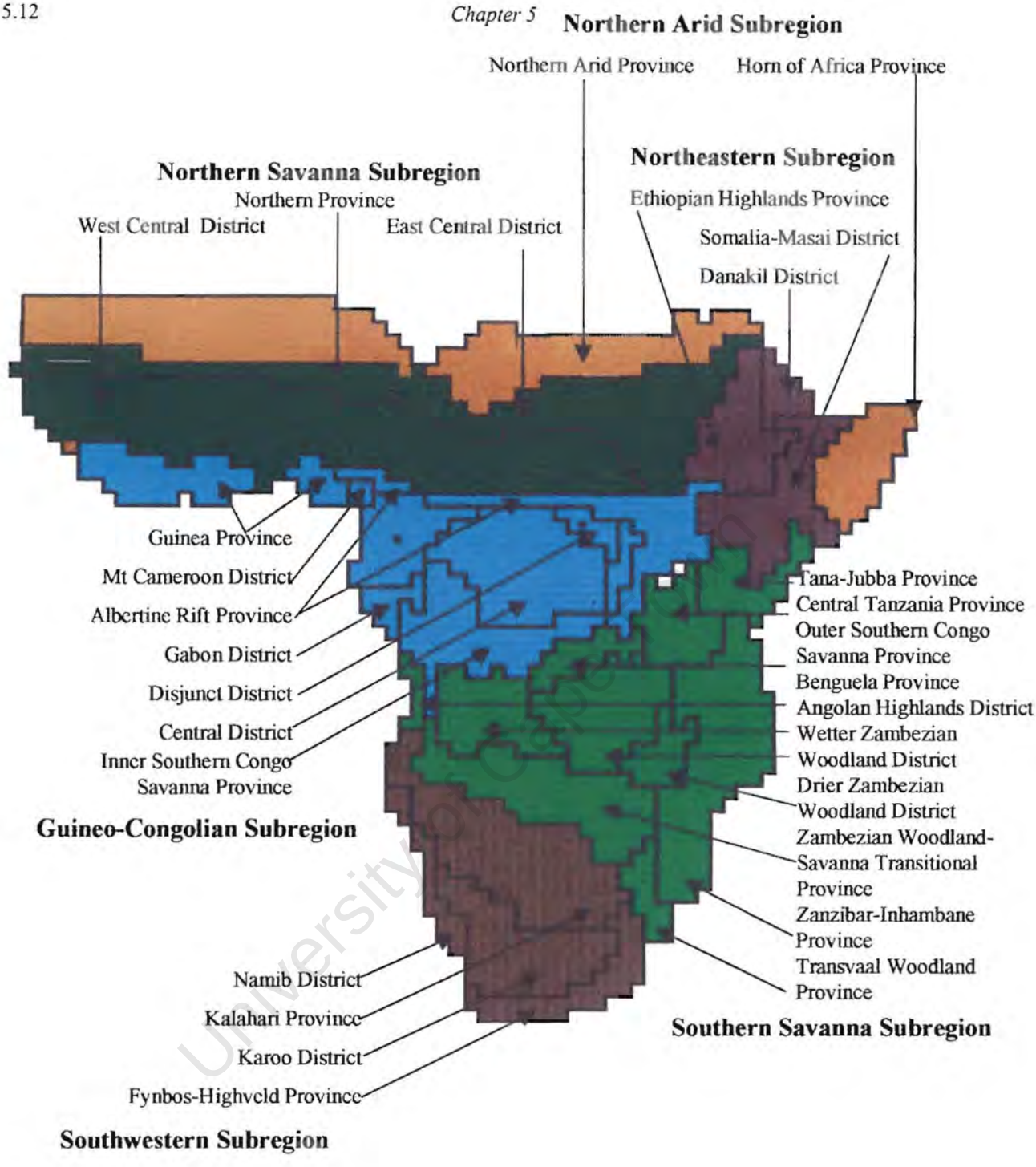

Figure 5.3.a. Patterns of distribution as defined by cluster analysis for terrestrial endemic Afrotropical passerine bird species.

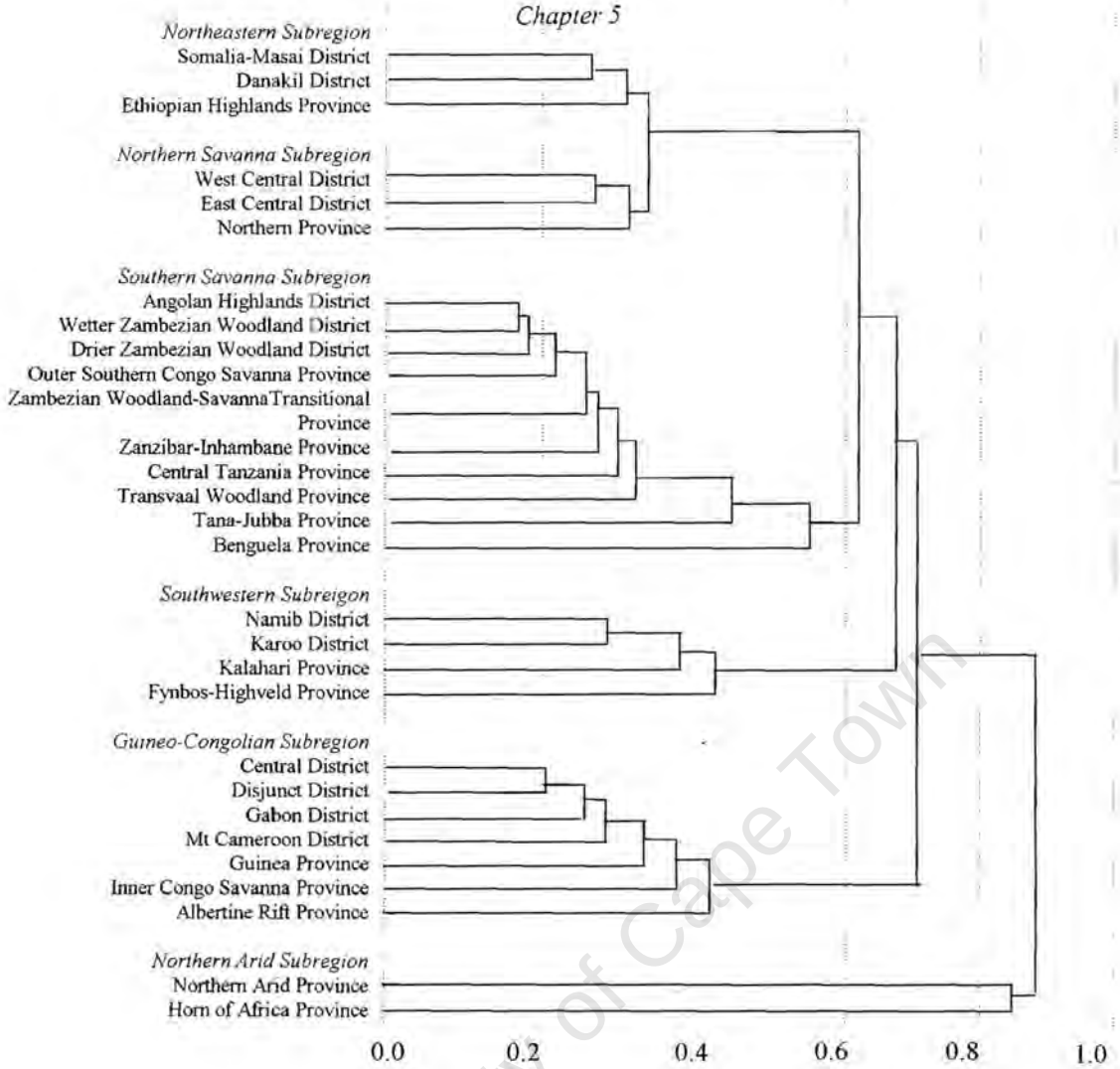

Figure 5.3.b. Relations of avifaunal zones defined by a cluster analysis on presence data for 1010 terrestrial endemic Afrotropical passerine bird species.

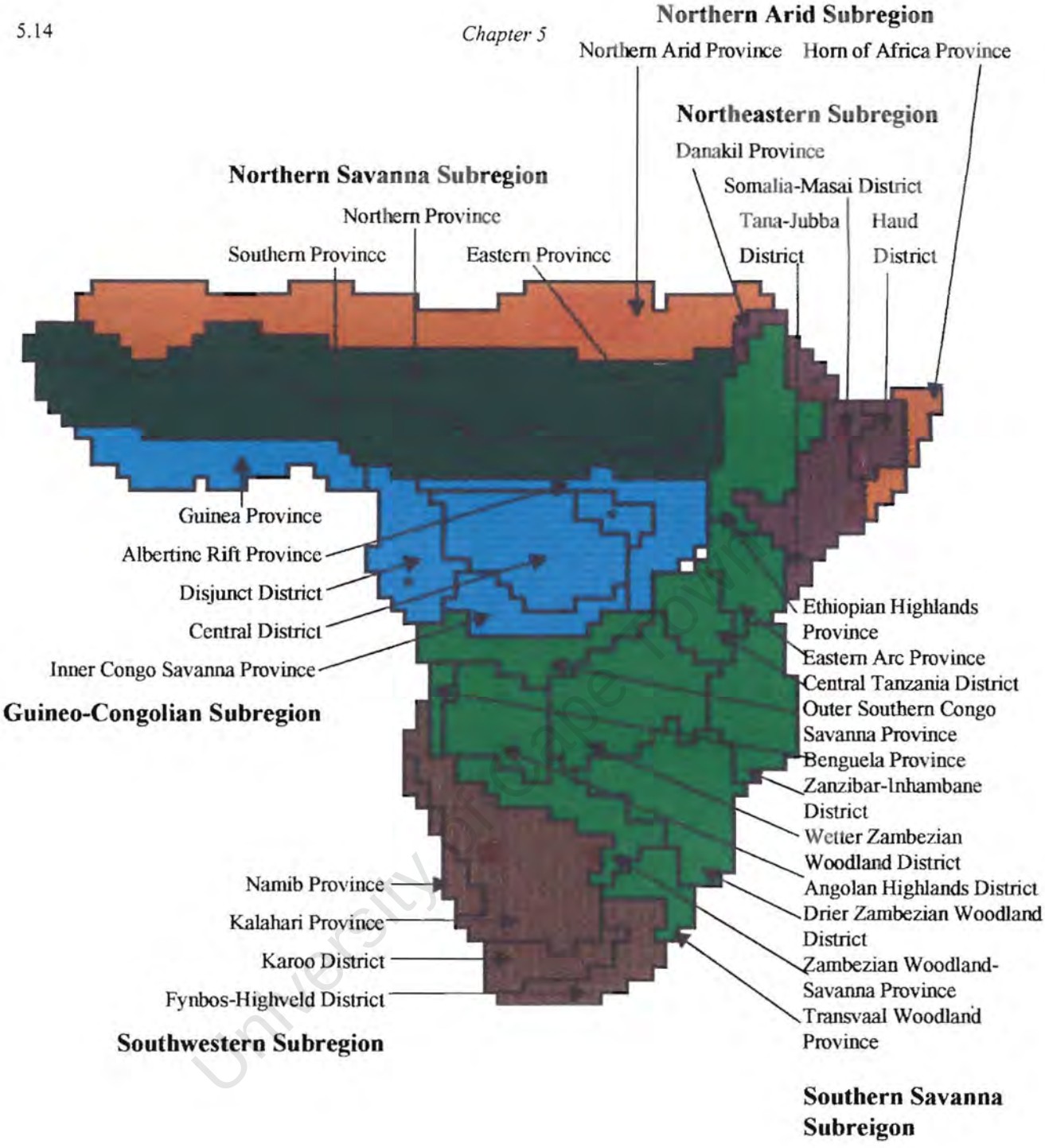

Figure 5.4.a. Patterns of distribution as defined by cluster analysis for terrestrial endemic Afrotropical nonpasserine bird species.

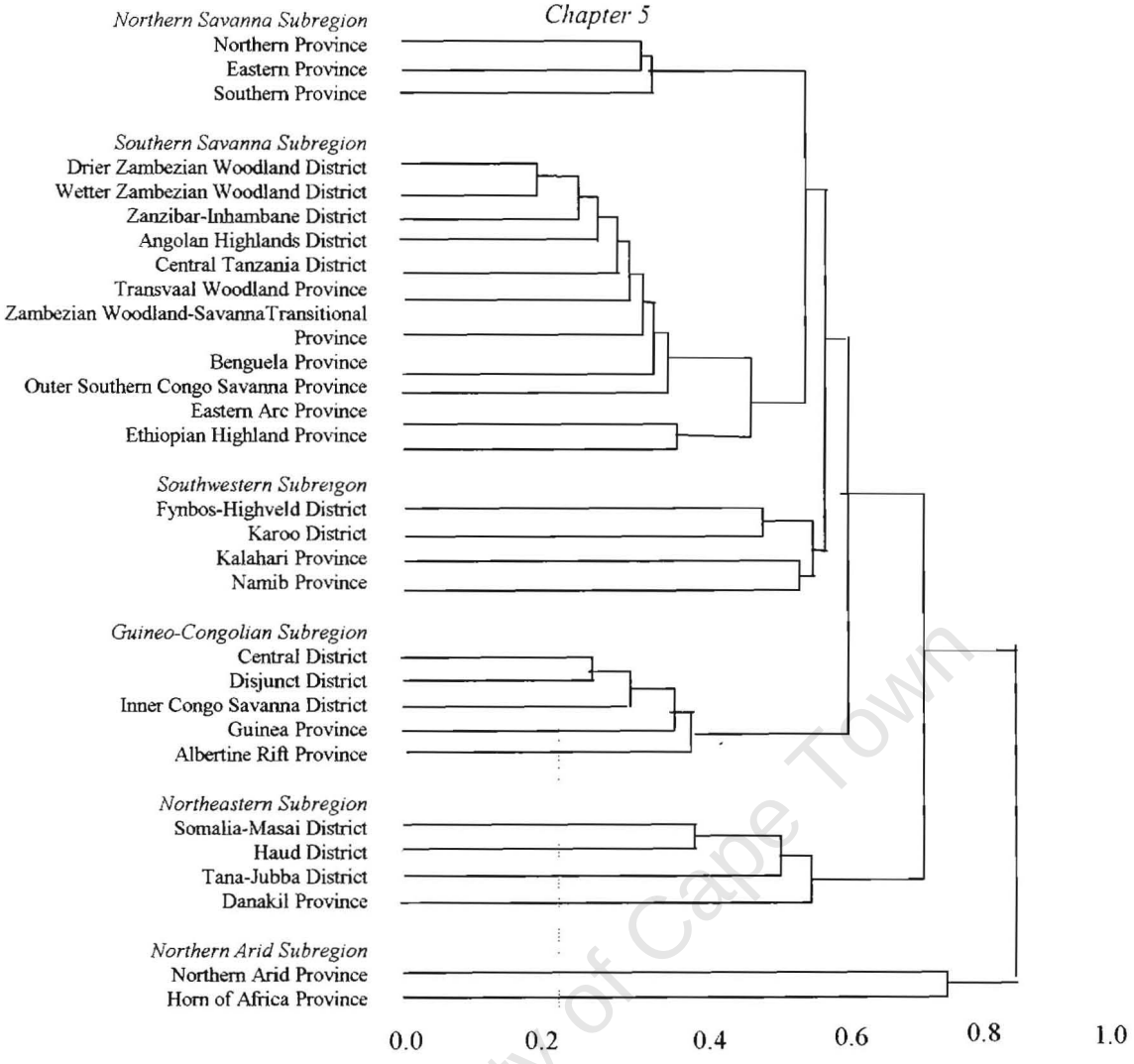

Figure 5.4.b. Relations of avifaunal zones defined by a cluster analysis on presence data for 427 terrestrial endemic Afrotropical nonpasserine bird species.

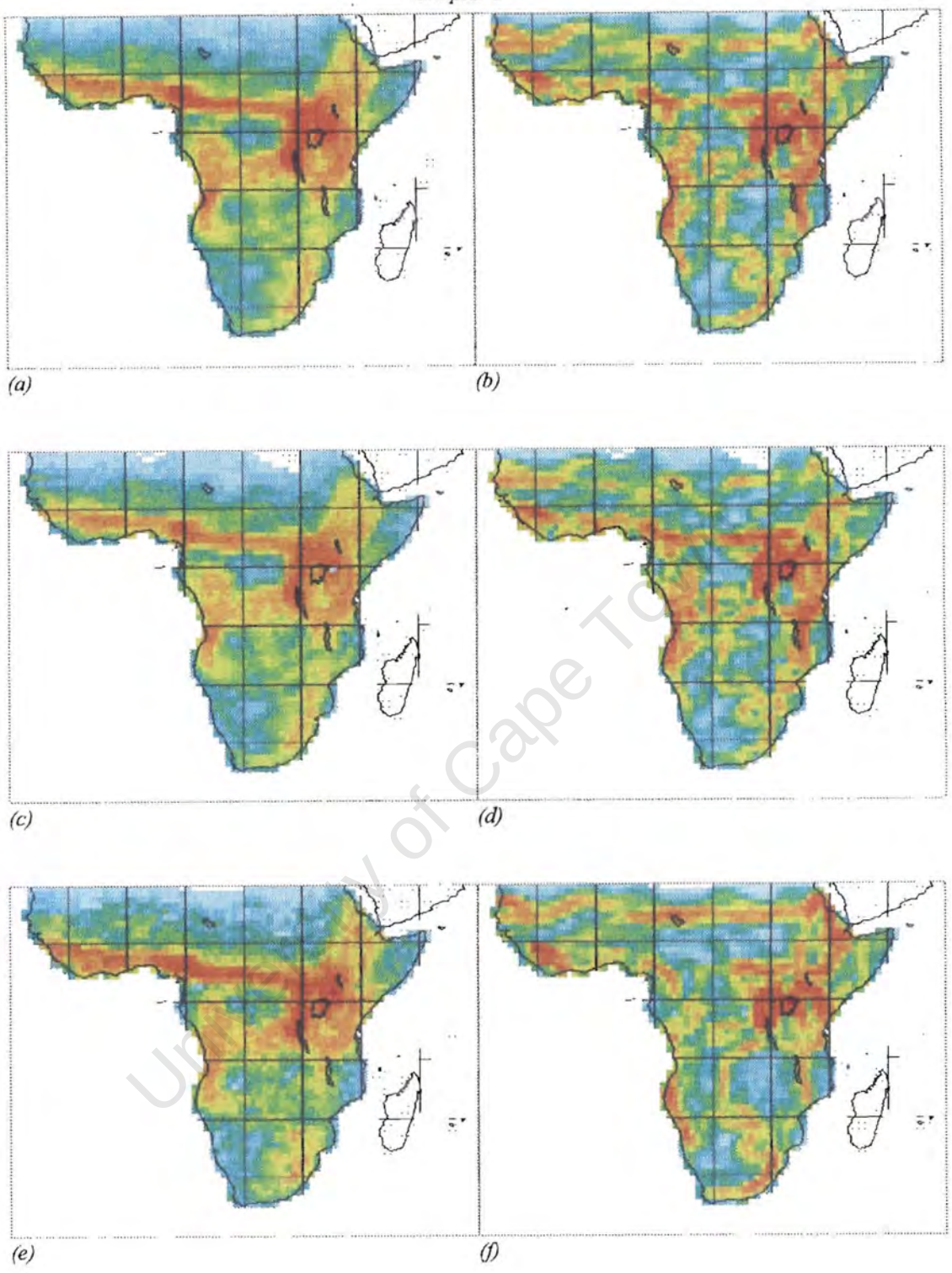

Figure 5.5. Patterns of species replacement (as measured by neighbourhood segregation) and species richness gradients (as measured by neighbourhood heterogeneity) for all endemic Afrotropical (a & b), passerine (c & d), and nonpasserine (e & f) bird species.

nonpasserines). Most are defined at a Bray-Curtis distance (BC) of between 0.4 and 0.5 (Fig. 5.2b for all Afrotropical endemics; Fig. 5.3b for endemic passerines; Fig. 5.4b for endemic nonpasserines), with the exception of the Northern Arid Subregion which forms a cluster at 0.75. Note that because Bray-Curtis is a *distance* measure, the *smaller* the figure, the *greater* the similarity. The Northeastern (BC = 0.50), Northern Savanna (BC = 0.52) and Southern Savanna (BC = 0.46) Subregions are closely related. The Northeastern and Northern Savanna Subregions cluster at BC = 0.53. The Southern Savanna Subregion joins the latter cluster at BC = 0.57. The Guineo-Congolian Subregion (BC = 0.45) follows somewhat more distantly at BC = 0.60, followed by the Southwestern Subregion (BC = 0.43) at BC = 0.65, and finally the Northern Arid Subregion (BC = 0.84) at BC = 0.88. Subregions broadly coincide with major Phytochoria as identified by White (1983) (Fig. 5.5, Table 5.2). Each subregion is subdivided into a number of districts, ranging from two (Northern Arid Subregion) to ten (Southern Savanna Subregion), totalling 36 districts across the six subregions.

Complete lists of characteristic and zone-restricted (based on terrestrial Afrotropical endemics) are given in Appendix 5.1 for each zone. Note that all characteristic species are, by definition, zone-restricted, and so are not repeated in the lists of zone-restricted species. Note also that all species restricted to a district will also be restricted to their respective province and subregion, and so for brevity's sake are only listed under the smallest zonal unit (e.g. district or province) to which they are restricted and are not repeated in the lists for larger zonal regions (e.g. province or subregion).

Passerines do not subdivide the Afrotropical region more finely than the nonpasserines (Figs. 5.3 & 5.4). Passerines and nonpasserines define approximately the same number of zones (Figs. 5.3 & 5.4). However, the passerines do define one extra zone in the Guineo-Congolian Subregion that the nonpasserines do not define, namely the Gabon District. On the other hand, nonpasserines define the southern forest-savanna transition as consisting of two clear parts (*viz.* the Inner Southern Congo Savanna District in the Guineo-Congolian Subregion and the Outer Southern Congo Savanna Province in the Southern Savanna Subregion) which is congruent with the studies of Chapin (1932) and Lynes (1938).

Table 5.2. Vegetational composition (White's Phytochoria of 1983) of avifaunal subregions measured as number of one-degree grid cells (Total) and proportion of total subregion area (%) covered by a particular Phytochorion. Values that constitute more than 25 percent of the total area of a particular subregion are highlighted. All values are approximate as the scale of analysis was course.

Subregion	Northeastern		Northern Savanna		Southern Savanna		Guineo-Congolian		Southwestern		Northern Arid	
No. 1° grid cells/subregion	162		552		467		319		228		211	
White's (1983) Phytochoria	Total	*(%)*	Total	*(%)*	Total	*(%)*	Total	*(%)*	Total	*(%)*	Total	*(%)*
Afromontane	**40.5**	***25.0***	2.7	*0.5*	13.9	*3.0*	6.9	*2.2*	3.0	*1.3*	-	-
Somali-Masai	**99.7**	***61.5***	0.9	*0.2*	27.0	*5.8*	2.3	*0.7*	-	-	30.8	*14.6*
Sahara	-	-	2.9	*0.5*	-	-	-	-	-	-	**109.7**	***52.0***
Sahel	2.1	*1.3*	**144.7**	***26.2***	-	-	-	-	-	-	**64.5**	***30.6***
Sudanian	4.0	*2.5*	**287.3**	***52.1***	-	-	8.9	*2.8*	-	-	-	-
Zambezian	-	-	-	-	**308.4**	***66.0***	1.1	*0.3*	19.6	*8.6*	-	-
Lake Victoria	-	-	-	-	4.8	*1.0*	16.8	*5.3*	-	-	-	-
Zanzibar-Inhambane	4.1	*2.5*	-	-	26.4	*5.7*	-	-	-	-	-	-
Tongaland-Pondoland	-	-	-	-	12.9	*2.8*	-	-	1.6	*0.7*	-	-
Guinea-Congolia/ Zambezia	-	-	-	-	45.3	*9.7*	18.4	*5.8*	-	-	-	-
Guineo-Congolian	-	-	11.1	*2.0*	-	-	**224.7**	***70.4***	-	-	-	-
Guineo-Congolian/ Sudanian	-	-	87.3	*15.8*	-	-	12.5	*3.9*	-	-	-	-
Kalahari-Highveld	-	-	-	-	6.4	*1.4*	-	-	**108.0**	***47.4***	-	-
Karoo-Namib	-	-	-	-	-	-	-	-	**60.0**	***26.3***	-	-
Cape	-	-	-	-	-	-	-	-	6.7	*2.9*	-	-

The passerines only define one large southern forest-savanna transition zone within the Guineo-Congolian Subregion and a very small, fragmented forest-savanna transition zone in the Southern Savanna Subregion. The ordering of districts within subregions, and the relation of subregions to each other, differs between passerines and nonpasserines, but these differences are probably not significant. Most districts, provinces, and subregions are defined at similar BC values by passerines and nonpasserines, although the passerines do define the Southwestern and Northeastern Subregions more strongly (Figs 5.4a & b).

Results of turnover analyses (both species replacement and species richness gradients) retrieve all

subregional boundaries and many provincial and district boundaries. The sharp transition between the Guineo-Congolian and Northern Savanna Subregions is reflected by a saturated, narrow band of species replacement along the entire length of the boundary (Figs. 5.5 a,c,e). The species gradient seen between the Guineo-Congolian and Northern Savanna Subregions, merely reflects how much more species rich the Guineo-Congolian Subregion is than the Northern Savanna Subregion, rather than indicating that the Northern Savanna is merely a depauparate subset of the Guineo-Congolian Subregion. Interestingly, this richness gradient is more pronounced in the passerines than the nonpasserines, probably due to the super-abundance of forest passerines. Replacement plots show that the southern forest-savanna transition is more diffuse and broader than the northern forest-savanna transition (Figs. 5.5a,c,e). Richness gradient plots show that this transition is somewhat tiered (Figs. 5.5b,d,f). The eastern boundary of the Guineo-Congolian Subregion represents a complex intermingling of a number of avifaunas, showing both high replacement (Figs. 5.5a,c,e) and gradient (Figs. 5.5b,d,f) values. The high replacement and gradient values between the Ethiopian Highland Province and the Northern Savanna Subregion, and between the Ethiopian Highland Province and the Horn of Africa Province of the Northern Arid Subregion, probably reflect the uniqueness of the Ethiopian Highland Province avifauna. Note that values are higher for the nonpasserines, which tend to give greater emphasis to the Ethiopian Highlands in terms of total species richness and narrow endemism than do the passerines (compare Figs. 3.1m & n and k & l, and Figs. 3.4c and 3.3c). Richness gradients also distinguish between the Ethiopian Highland Province and Somalia-Masai District of the Northeastern Subregion, and between the Somalia-Masai District of the Northeastern Subregion and the Horn of Africa Province of the Northern Arid Subregion (Figs. 5.5b,d,f), indicating a steady decline in species richness from the Ethiopian Highlands towards the arid Somali coast. The boundary between the Northern Savanna and the Northern Arid Subregions is primarily due to richness gradients (Fig 5.5b). The boundary between the Southern Savanna and Southwestern Subregions is partly due to replacement, and partly due to richness gradients (compare Figs. 5.5a,c,e and Figs. 5.5b,d,f). Specifically, quite high replacement and gradient values are seen between the Southwestern Subregion and the Tonga-Pondoland Province of the Southern Savanna Subregion, with gradient values in this area being higher for nonpasserines than passerines. Within the Southern Savanna

Subregion medium levels of replacement are seen between the Angolan Highlands and Wetter Zambezian Wooldand Districts, between the Wetter and Drier Zambezian Wooldand Districts, and between the latter districts and the Zanzibar-Inhambane District. The high gradient values seen between the Angolan Highlands and Wetter Zambezian Wooldand Districts shows that the Angolan Highlands District is really just a depauparate subset of the Wetter Zambezian Wooldand District avifauna. Note that the boundary between the Wetter and Drier Zambezian Wooldand Districts is dominated by replacements, with virtually zero gradient values, indicating two distinct avifaunas (compare Figs 5.5 a and b). The apparent contribution of species gradients to the boundaries between the latter districts and the Zanzibar-Inhambane District, and between the Central Tanzania and the Zanzibar-Inhambane Districts, is in fact a reflection of the high band of species richness that runs from the Eastern Arc mountains to those of western Mozambique and eastern Zimbabwe. This apparent gradient is particularly apparent in the passerines due to the speciose passerine montane forest fauna. High replacement along the Angolan Escarpment, emphasises the difference between the escarpment and Angolan Highlands District avifaunas, and to a lesser extent the difference between the avifaunas of the Angolan Escarpment and the Benguela Province. High gradient values in this regions highlights the depauparate nature of the Benguela Province avifauna. It also shows a drop-off in species richness between the Angolan Escarpment and the Angolan Highlands District. Within the Southwestern Subregion, fairly high gradient values between the Namib Province and the inland zones (Karoo District and Kalahari Province) highlights the depauparate nature of the Namib Province. Note that the gradient values are slightly lower in the passerines due to a few larks restricted to the Namib Province (see Appendix 5.1). These species are also responsible for the slight replacement values seen in between the Namib Province and the inland zones in the passerines, which are absent in the nonpasserines. The boundary between the Fynbos and Karoo Districts are marked by medium levels of both replacement and gradients. This effect is at least in part due to the subtropical subtraction effect of coastal (particularly forest) forms that extend to varying degrees along the South African coastline from the Southern Savanna Subregion. This effect is also seen in other biota (e.g. small mammals: Gelderblom & Bronner 1995). The boundary is more pronounce in nonpasserines than passerines due to the higher species complement of passerines in the Karoo.

Table 5.3. Zone area, absolute, percentage and relative species richness, and number, percentage and relative number of endemics, and number of characteristics species per avifaunal zone. Percentage species richness (% spp rich) and zone-restricted species richness (% end) are proportional to all species in the database (1437). Relative species richness (Rel spp rich) and relative zone-restricted species richness (Rel end) are proportional to the respective avifaunal zone size. (# cells/zone).

zone name	*# cells/ zone*	*spp rich*	*% spp rich*	*Rel spp rich*	*# ends*	*% end*	*Rel end*	*# chars*
Northeastern Subregion								
Somalia-Masai	53	344	23.96	6.49	7	0.49	0.13	0
Tana-Jubba	19	391	27.23	20.58	3	0.21	0.16	0
Lake Turkana	22	480	33.43	21.82	5	0.28	0.18	1
Ethiopian Highlands	51	411	28.62	8.06	25	1.74	0.49	3
Danakil	17	199	13.86	11.71	1	0.07	0.06	0
Northern Savanna Subregion								
West Central	191	395	27.51	2.07	4	0	0	3
East Central	112	354	24.65	3.16	1	0.07	0.01	0
Southeastern	57	432	30.08	7.58	3	0.14	0.04	0
Southwestern	51	541	37.67	10.61	5	0.35	0.10	0
Northern	141	227	15.81	1.61	1	0.07	0.01	0
Southern Savanna Subregion								
Drier Zambezian Woodland	87	535	37.26	6.15	9	0.35	0.06	0
Wetter Zambezian Woodland	75	483	33.64	6.44	4	0.28	0.05	0
Zanzibar-Inhambane	70	433	30.15	6.19	2	0.14	0.03	1
Angolan Highlands	48	420	29.25	8.75	3	0.07	0.02	0
Central Tanzania	30	503	35.03	16.77	4	0.21	0.10	0
Zambezian Woodland-Savanna Transition	40	350	24.37	8.75	0	0	0	0
Eastern Arc	37	664	46.24	17.95	36	2.16	0.84	0
Outer Southern Congo Savanna	48	550	38.30	11.46	7	0.35	0.10	0
Tongaland-Pondoland	29	393	27.37	13.55	4	0.14	0.07	0
Benguela	3	207	14.42	69.00	1	0	0	
Guineo-Congolian Subregion								
Central	96	438	30.50	4.56	3	0.28	0.04	0
Disjunct	36	473	32.94	13.14	3	0	0	0
Gabon	27	376	26.18	13.93	1	0.07	0.04	0
Mt Cameroon	6	417	29.04	69.50	4	0.28	0.67	0
Inner Southern Congo Savanna	40	456	31.75	11.40	0	0	0	0
Lower Guinea	11	319	22.21	29.00	0	0	0	0
Upper Guinea	47	414	28.83	8.81	10	0.70	0.21	3
Ubangi-Uelle Savanna	12	345	24.03	28.75	0	0	0	0
Albertine Rift	44	835	58.15	18.98	48	3.13	1.02	0
Southwestern Subregion								
Highveld	24	296	20.61	12.33	2	0.07	0.04	0
Karoo	53	211	14.69	3.98	2	0.14	0.04	2
Fynbos	19	215	14.97	11.32	2	0.14	0.11	5
Kalahari	112	420	29.25	3.75	9	0.35	0.04	1
Namib	20	174	12.12	8.70	2	0.07	0.05	0
Northern Arid Subregion								
Northern Arid	171	94	6.55	0.55	0	0	0	0
Horn of Africa	40	148	10.31	3.70	6	0.42	0.15	1

The subregions are discussed primarily based on results from the terrestrial Afrotropical endemics database, and in the order in which they join the dendrogram. Note that discussion, particularly comparisons with other studies and possible evidence for speciation barriers and refugia, specific to each avifaunal zone is included in the results under the heading of 'general points'. This format was adopted to avoid unnecessary repetition and to keep certain discussion points close to the relevant result sections as the contents of the results are quite voluminous and separation of discussion from relevant results leads to a loss of information flow. Pertinent issues arising from the results (and 'general points') section are summarised in a general discussion which is presented after the results section.

5.3.1. Northeastern Subregion

LOCATION AND AVIFAUNA

This subregion encompasses a phenomenal altitudinal range from below sea level in the Danakil depression to over 4000m in the Ethiopian Highlands. It stretches from Eritrea in the north to Malindi on the Kenyan coast in the south, and from the Haud (Ogaden) Plateau in the east to Lake Turkana in the west. It is no surprise that the vegetation of this subregion varies from true desert to humid forest. This variety of habitat types accommodates 58 zone-restricted species. Over half of these species are restricted to the Ethiopian Highland Province. This results in the highlands forming a cluster discrete from the four lower altitude districts, namely the Somalia-Masai, Tana-Jubba, Lake Turkana and Danakil Provinces. The districts of the Lowland Province (namely the Somalia-Masai, Tana-Jubba, Lake Turkana Districts) are identified as quite different to the Ethiopian Highlands District (BC = 0.469 dissimilarity; Fig 5.2b). The strong affinity of the three lowland districts to each other is attributable to a number of species that are distributed in the dry and arid *Acacia* thorn scrub and savanna (White (W) 42: Somali-Masai *Acacia-Commiphora* deciduous bushland and thicket) that sweeps from the Gulf of Aden on the Red Sea coast, around the southern base of the Ethiopian Highlands through Somalia, then south and westwards to Lake Turkana (e.g. *Emberiza poliopleura*). A number of the species characteristic of the *Acacia* thorn scrub and savanna extend northwards from Lake Turkana into the rift valley that bisects

the Ethiopian Highlands (e.g. *Anthoscopus musculus* and *Uraeginthus ianthinogaster*), and from the Ethiopian foothills eastwards into the 'Horn of Africa' District of the Northern Arid Subregion (e.g. *Merops revoilii* and *Nectarinia hunteri*), or southwards into the Central Tanzania District of the Southern Savanna Subregion (e.g. *Pterocles decoratus*, *Eurocephalus rueppelli*, and *Turdoides rubiginosus*).

5.3.1.1. Somalia-Masai District

LOCATION AND AVIFAUNA

This district largely covers the land southeast of the Ethiopian Highlands as far as, and including, the Haud Plateau, from the Gulf of Aden on the Red Sea coast in the north, to Muqdisho on the Somali coast in the southeast, and to the Kenyan towns of Garissa and Marsabit in the southwest. In the south a strip along the Jubba River projects from the Tana-Jubba District into the Somalia-Masai District between Muqdisho and Garissa. Although vegetationally dominated by Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (W 42), after which it is named, a look at habitat preferences of the seven zone-restricted species shows a wide variety. The list includes riparian woodland (*Streptopelia reichenowi*), highland grassland (*Heteromirafra archeri*), dry bush and thorn scrub (*Mirafra aloplex*), arid and rocky habitats (*Mirafra sharpii* and *M. degodensis*), and red desert soil (*M. ashi*). This indicates a substantial range of habitats in an area that is often misconceived to be very uniform (see Archer & Godman 1937 for an informative description of the vegetation and birdlife of this area).

5.3.1.2. Tana-Jubba District

LOCATION AND AVIFAUNA

The Jubba and Tana Rivers, after which the district is named, form its northeastern and western boundaries. The southern boundary is demarcated by Malindi on the Kenyan coast and the Tsavo National Parks in the interior. The vegetation is dominated by the Zanzibar-Inhambane East African coastal mosaic (W 16a). This district also includes the forest patches (W 16b) north of the Arabuko-Sokoke such as those stretching up along the Tana River (*Tauraco fischeri*). The Tana River also flows through arid bush (*Cisticola restrictus*). Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (W 42) is also found in this district. The third zone-restricted species of this district, *Campethera*

mombassica, utilizes both the forest and woodland habitats.

5.3.1.3. Lake Turkana District

LOCATION AND AVIFAUNA

The district is centred around Lake Turkana, stretching from Negele, southern Ethiopia, in the east, to Kidepo National Park on the Uganda-Kenya border in the west, and to Mt Nyiru in the south. It is typified by the distributional range of *Tockus jacksonii* that inhabits the *Acacia* savanna that occurs broadly in this area. The northeastern portion of the Lake Turkana District covers a range of vegetation types and altitudes, providing habitats for a number of range-restricted specialists, from the lower altitude *Acacia* savanna specialist *Zavattariornis stresmanni*, through *Hirundo megaensis* an aerial forager which prefers mid-altitude *Acacia* savanna and short grassland, to the montane species *Heteromirafra sidamoensis* and *Tauraco ruspolii*, which inhabit montane grassland and evergreen Juniper forest, respectively.

GENERAL POINTS

The northeastern portion of the Lake Turkana District corresponds with Urban and Brown's (1971) 'South East' area in Ethiopia. This dry open bushed and wooded country of northeastern Kenya and southern Somalia is separated from similar habitat in northeastern Uganda, southern Sudan, central Ethiopia, and northwestern Kenya by an area of short grass plains on the black lava soils east of Lake Turkana (which accommodates the very localized *Mirafra williamsi)*. Muriuki *et al.*'s (1997) study of Kenyan avifauna at a quarter of a degree square scale (30 x 30 mins) identified these three entities as separate avifaunal zones.

Lake Turkana benefits from the influx of Southern Savanna species (e.g. *Francolinus hildebrandti*, *Merops bullockoides*, *Sylvietta whytii*, and *Eremopterix leucopareia*) and Northern Savanna species (e.g. *Ptilopachus petrosus*, *Tauraco leucolophus*, *Circaetus pectoralis*, *Ploceus heuglini*, and *Estrilda troglodytes*) resulting in a higher total, percentage, and relative species richness than the Ethiopian Highlands (Table 5.3). However, the Ethiopian Highlands clearly has a much higher number of unique

(zone-restricted) species.

5.3.1.4. Ethiopian Highlands Province

LOCATION AND AVIFAUNA

The plateau areas of the highlands are clothed in grassland (some of which is seasonally swampy), *Podocarpus* and broad-leaved evergreen forests, graduating through Hagenia and St. John's Wort forest and bamboo thickets at the sub-afroalpine level, to the Giant Lobelia and Everlastings of the afroalpine level (Urban 1980). The majority of the species restricted to this province are found in the montane forest (*Francolinus castaneicollis*, *Tauraco leucotis*, *Zosterops poliogaster*, and *Agapornis taranta*), including Podocarpus (*Poicephalus flavifrons* and *Asio abyssinicus*) and Juniper (*Cisticola bodessa*, *Dendropicos abyssinicus*, and *Oriolus monacha*). Others occupy woodland (*Serinus reichardi* and *Parus leuconotus*), grassland (*Estrilda ochrogaster*, *Vanellus melanocephalus*, and *Macronyx flavicollis*) and rocky areas or cliffs (*Corvus crassirostris*, *Columba albitorques*, *Myrmecocichla melaena*, *Onychoganthus albirostris*, and *Serinus ankoberensis*). At higher altitudes, *Parophasma galinieri* utilizes forest and bamboo, while *Serinus nigriceps* uses moor- and heathlands.

GENERAL POINTS

This province corresponds with the 'Western and Southeastern Highlands' of Urban and Brown (1971), which they define as all areas above 2000m (plus montane forests down to 1500m of Keffa and Illubabor), excluding the river gorges of the Blue Nile, Abbai, Tekkeze, and Omo, which deeply incise the western plateau. The latter are considered to form part of the 'West Ethiopia' area, which comprises the Sudanese lowlands and northern Eritrea (Urban & Brown 1971). The scale of one-degree square used in this study is too coarse to distinguish between Urban and Brown's (1971) 'true' highland as defined above, and its associated river gorges. This can be seen in the identification of *Francolinus harwoodi* as a zone-restricted species of the Ethiopian Highland Province; this species is typically restricted to the Typha beds of the Blue Nile gorge. Most species occur on both mountain blocks with only a few being restricted to the western block, namely *Myrmecocichla melaena* and the recently discovered *Camprimulgus solala*.

5.3.1.5. Danakil Province

LOCATION AND AVIFAUNA

This province encompasses Somalia-Masai semi-desert grassland and shrubland (W 45b) and regs, hamadas and wadis (W 71) of the Danakil depression, the Red Sea coast and neighbouring hills. It also includes the northern limits of the Chercher Highlands on which Juniper forest occurs. This provides habitat for the only species restricted to this zone, namely *Francolinus ochropectus*. The Danakil Province differs from the other lowland districts in its more arid nature. In addition, a few lowland species of the Ethiopian Highlands Province extend into the Danakil depression (*Cisticola bodessa* and *Turdoides leucopygius*) further increasing the difference between it and the other three lowland zones. This depauparate mixture of lowland and highland elements result in it being defined as the zone most dissimilar from the other Northeastern Subregional zones. It is defined as a strongly as the Ethiopian Highlands Province (both with a BC = 0.36).

GENERAL POINTS

This district corresponds well with the 'North-East Ethiopia' region of Urban and Brown (1971).

SPECIATION PATTERNS WITHIN THE NORTHEASTERN SUBREGION

Speciation events in the Lake Turkana District seem to be connected to the lower reaches of the Ethiopian Highlands in the south, with a member each of two separate superspecies pairs being restricted to these foothills (*Tockus* [*deckeni*] *jacksoni* and *Hirundo* [*dimidiata*] *megaensis*), their respective superspecies mates occurring in either the *Acacia-Commiphora* wooded steppe to the east of this district (*T. [deckeni] deckeni*) or the savannas of the Northern and Southern Savanna Subregions (*H. [dimidiata] leucosoma*). These foothills (of less than 2000m) were recognised by Urban and Brown (1971) as a distinct avifaunal entity within Ethiopia, *viz* 'South Ethiopia', which they described as 'generally similar to the areas of northern Kenya' (Urban & Brown 1971). This is echoed by Muriuki *et al.* (1997) who noted that the avifauna of the dry bushed and wooded country of northeastern Kenya extends to southern Somalia and southeastern Ethiopia. This latter zone was separated from the dry bush country of northwestern Kenya (which extends into northeastern Uganda, southern Sudan, and southwestern Ethiopia) by a zone of short

grass plains on black lava soils just east of Lake Turkana, which accommodates the very localized *Mirafra williamsi* (Muriuki *et al.* 1997).

The topography and vegetation the three lowland zones appear fairly uniform and do not seem to provide any clear opportunities for allopatric speciation events. However, each has a number of zone-restricted species. Although the Somali-Masai District is vegetationally dominated by Somali-Masai Acacia-Commiphora thicket (W 42), after which it is named, a look at the habitat preferences of its seven zone-restricted species shows a variety of habitats, as discussed above. There have been two superspeciation events in the Somali-Masai District between the very arid coastal steppe and the *Acacia-Commiphora* wooded steppe of the Haud (which extends into the Ethiopian Rift Valley and Northern Savanna Subregion) in the form of *Streptopelia* [*decaoto*] *reichenowi* and *roseagrisea*, and *Mirafra* [*africanoides*] *aloplex* and *africanoides*. The northern Somalia mountains of the Golis range and Warsengalia may have acted as a vicariance barrier between *Mirafra* [*africana*] *sharpi*, which is restricted to the very narrow coastal strip of northern Somalia, and *africana*, which occurs in both the Northern and Southern Savanna Subregions. Interestingly, these mountains did not act as a vicariance barrier to *S. reichenowi*, which occurs from the northern Somali coast to the Dawa tributary (5°N, 39°5'E) of the Jubba River. In the Tana-Jubba District, two superspecies pairs, namely *Campethera* [*notata*] *mombasica* and *abingoni*, and *Tauraco* [*persa*] *fischeri* and *persa*, meet around 5°S, indicating a possible break in the coastal forest-savanna mosaic in this region. The superspecies pair of *Cisticola* [*subruficapillus*] *restrictus* and *lais* indicate that the coastal forest-savanna mosaic may have been very restricted at some point, with the *restrictus* only occurring on the lower reaches of the Tana River and *lais* being restricted to the coast some considerable distance to the south. However, this example is not conclusive as the *subruficapillus* superspecies contains other species, which seems to indicate a complex pattern of vicariant speciation in this superspecies.

5.3.2. Northern Savanna Subregion

LOCATION AND AVIFAUNA

This subregion starts as a thin strip at the Red Sea coast north of Eritrea. It then stretches south around the western foothills of the Ethiopian Highlands from where it runs broadly westwards across north Africa roughly between 5 and 15°N to the west coast. It is the second mostly weakly defined subregion at BC = 0.52, being a region of generally low species richness, excepting local peaks in the Bameda Highland in the south, and on the Gambian coast in the west.

Subdivision of the Northern Savanna Subregion closely follows the bands of vegetation that stretch the entire breadth of the continent, from the northerly Sahel *Acacia* wooded grassland and deciduous bushland (W 34) through Sudanian undifferentiated woodland (W 29a) to the southerly Sudanian woodland with abundant *Isoberlinia* (W 27). The Sudanian woodland with abundant *Isoberlinia* (W 27) does not run due west-east, and shows a marked southeastern extension to a pocket of Sudanian undifferentiated woodland (W 29a) which extends to the banks of Lake Victoria. This southeastern extension is seen in many bird species that occupy various portions of the Northern Savanna Subregion, namely *Coracias cyanogaster*, *Myrmecocichla albifrons*, *Nectarinia coccinogastra*, and *Euschistospiza dybowskii*.

GENERAL POINTS

Despite the low species richness of terrestrial endemic species that the Northern Savanna Subregion shows relative to the neighbouring Northeastern and Guinea-Congolian Subregions, the Northern Savanna Subregion represents a distinct avifauna with a number of species that are unique to it (characteristic and zone-restricted species). In addition, it exhibits a high degree of species replacement along its southern border with the Guineo-Congolian Subregion (Fig. 5.5a), indicating that as one moves north from the Guineo-Congolian forest, the forest avifauna is replaced by a savanna avifauna, rather than the Northern Savanna Subregion merely being a depauparate subset of what is found in the Guineo-Congolian Subregion. The band of high relative replacement on the northern border of the Northern Savanna Subregion in the database representing all terrestrial species (Williams *et al.* in press.) is due to

lateral replacement of savanna species that reach their northern boundaries in different places (compare *Struthio camelus* with *Turdoides fulvus*, or *Neotis nuba* and *Necrosyrtes leucopyga*), rather than indicating the replacement of the northern savanna avifauna by a strongly distinct desert avifauna.

The Northern and Southern Savanna Subregions, as represented in the cluster analysis based on endemic terrestrial species, do not meet at Paleo-Sudd, which was suggested to be the primary vicariance feature between the Northern and Southern Savannas by Crowe and Crowe (1982) and Crowe and Kemp (1986). However, the role of Paleo-Sudd as a vicariance agent (e.g. *Turtur* [*chalcospilos*] *abyssinicus* and *chalcospilos*), or possibly as a dispersal barrier (to both Northern Savanna, e.g. *Lybius vieilloti*, and Southern Savanna forms, e.g. *Vanellus coronatus*, *Calamonastes simplex*, and *Nectarinia mariquensis*), cannot be ruled out. A slightly more southerly junction, between Lakes Victoria and Turkana coinciding with the southeastern extension of Sudanian undifferentiated woodland, is suggested by the distributional limits of both Southern Savanna species (e.g. *Creatophora cinerea* and *Cisticola chinianus*) and Northern Savanna species (e.g. *Pterocles quadricinctus* and *Muscicapa gambagae*). The development of the Rukwa Rift, still further to the south, may well have been an equally, or more important, vicariance event than Paleo-Sudd to the savanna groups, forming the meeting point of a number of savanna superspecies pairs, namely *Merops* [*nubicus*] *nubicus* and *nubicoides*, *Tricholaema [leucomelas] frontatus* and *diadematа*, *Urocolius* [*macrourus*] *macrourus* and *indicus*, and *Sylvietta* [*ruficapilla*] *ruficapilla* and *whytii*.

Although a large number of savanna species range through both savanna subregions (e.g. *Merops pusillus* and *Glaucidium perlatum*), these two subregions do not meet, and are separated by an area of complex topography and vegetation (consisting of the Albertine Rift Province of the Guineo-Congolian Subregion and the Lake Turkana District of the Northeastern Subregion), which forms the confluence point of a number of avifaunas (Fanshawe & Bennun 1991; Williams *et al.* in press). This observation is supported by the high values of species replacement and range edges in this area (Fig. 5.5a).

A number of species disperse south of Paleo-Sudd along the northeastern forest border (including species occurring in both savannas, e.g. *Lanius collaris* and *Anthreptes longuemarei*, and Southern Savanna forms extending a short distance into the Northern Savanna, e.g. *Nectarinia mariquensis* and *Ploceus bicolor*). This pattern is *contra* Crowe and Kemp (1986) whose study of galliform and hornbill evolution suggested that dispersal between the savannas was via Ethiopian or Somalia, rather than through the Sudd area of the Sudan. A few Northern Savanna forms endemic to the Afrotropics do show Crowe and Kemp's (1986) dispersal route (e.g. *Chelictinia riocourii*), but it is more prevalent in nonendemics (e.g. *Pterocles exustus*, *Cursorius cursor*, *Corvus ruficollis*, and *Eremopterix nigriceps*).

5.3.2.1. Central Province

LOCATION AND AVIFAUNA

A number of birds of arid thorn scrub and steppe stretch across the central 'band' of savanna-woodland in this subregion (*Vanellus tectus*, *Cisticola ruficeps*, and *Estrilda troglodytes*), resulting in the recognition of a Central Province consisting of the East Central and West Central Districts. A number of species that broadly follow this pattern extend into the Northern District (e.g. *Pterocles quadricinctus*).

GENERAL POINTS

The boundary between the East Central and West Central Districts within this province is probably due more to species reaching their western boundary here (e.g. *Cisticola troglodytes*) than western forms reaching their eastern boundary here. However, a number of woodland and savanna species that are primarily confined to the West Central District, but which follow the southeastern savanna extension to Lake Victoria, strengthen the divide between the two districts. The existence of a 'Mega-Chad', which possibly extended as far south as the Benue River (Crowe & Kemp 1986), may well have resulted in vicariant speciation of *Laniarius* [*barbarus*] *barbarus* and *erythrogaster*, *Batis* [*senegalensis*] *senegalensis* and *orientalis*, *Cisticola* [*rufus*] *rufus* and *troglodytes*, and *Eremomela* [*gregalis*] *pusilla* and *canescens*. However, the division between the West Central and East Central Districts coincides roughly with the disappearance of pockets of dry woodland in long grass savannas east of Lake Chad (e.g. *Poicephalus senegalus* and *Batis senegalensis*) and so the division could be attributed to subtle

differences in habitat and does not have to be interpreted as an influence of Mega-Chad.

5.3.2.1.1. East Central District

LOCATION AND AVIFAUNA

This district encompasses most of Sudan south of 15°N and the extreme west of Ethiopia. Vegetation ranges from *Acacia* grasslands and woodlands (W 43, 35b) in the north, to Sudanian woodland (W 27, 29a) and seasonally or permanently edaphic grasslands of 'tioch' and 'Sudd' (W 62, 61, 64) in the south (see Cave & Macdonald 1955 for a useful description of the vegetation divisions of Sudan). Of the two species restricted to this district, *Cisticola troglodytes* occurs through a broad range of grassy savannas with varying amounts of woodland, whilst *Ploceus badius* is found only in the riparian grassy savanna of the upper Nile.

5.3.2.1.2. West Central District

LOCATION AND AVIFAUNA

The West Central District stretches from just south of the Chad-Sudan border in the east, to Atlantic coast around the Gambia in the west, between ca 8°N and 15°N. There are no characteristic species and only three zone-restricted, namely *Streptopelia hypopyrrha*, *Cisticola rufus*, and *Estrilda caerulescens*. Savanna-woodland (W 29a, 27, 30) predominates in this district, although patches of swamps and edaphic grassland around Lake Chad (W 75, 63, 62) and of the Madara Plateau mosaic (W 33) do occur.

5.3.2.2. Southeastern Province

LOCATION AND AVIFAUNA

This forms the northeastern extent of lowland forest patches that reach into southwestern Sudan. It consists largely of a transition between the forest and grassland (W 11a) graduating into Sudanian woodland (W 27) that stretches into most of the Central African Republic. Both zone-restricted species, *Poicephalus crassus* and *Psalidoprocne mangbettorum*, are mainly found in forest patches and moist woodlands. This province is further supported by a number of species that nearly miss classification as zone-restricted species, in that they either range marginally into neighbouring districts (*Francolinus*

schlegelii, *Grafsia torquata*, and *Lagonosticta umbrinodorsalis*), or show the typical 'savanna arm' that extends south-eastwards to Lake Victoria (*Francolinus icterorhynchus* and *Tauraco leucolophus*).

5.3.2.3. Southwestern Province

LOCATION AND AVIFAUNA

This zone constitutes pieces of transitional vegetation between the Northern Savanna and Guineo-Congolian Subregions from the Bameda Highlands in the east to Guinea-Bissau in the west. It consists mostly of a forest-savanna transition (W 11a) with some mangroves (W 77) on the coast at the Dahomey Gap and in Guinea-Bissau. It corresponds well with Chapin's (1932) Upper Guinea Savanna District, although it also encompasses a small western portion of his Ubangi-Uelle Savanna District and his Cameroon Montane District, which dominates the avifauna of this district. Most of the zone-restricted species are endemic to the montane forest of the Bameda Highlands (*Tauraco bannermani*, *Columba sjostedti*, *Laniarius atroflavus*, *Malaconotus gladiator*, *Cossypha isabellae*, *Andropadus montanus*, *Phyllastrephus poensis*, *Phyllastrephus poliocephalus*, *Apalis bamedae*, and *Nectarinia oritis*). A few are savanna species, namely *Coccycolius iris* and *Malimbus ibadanensis*.

GENERAL POINTS

The fact that the Southeastern Province clusters quite a bit more strongly to the Central Province (BC = 0.319) than does the Southwestern Province (BC = 0.36) is somewhat puzzling, as few species of the Central Province extend their distributions into the Southeastern Province without also extending it into the Southwestern Province. In fact, there are only three examples that do so, namely *Circaetus pectoralis*, *Oenanthe heuglini*, and *Lamprotornis chalcurus*. Two Central Province species extend their ranges southwards into both the Southeastern and Southwestern Provinces, namely *Lamprotornis chloropectus* and *Turdoides plebejus*. Possibly more forest (Guineo-Congolian Subregion) species extend into the Southwestern Province than into the Southeastern Province, resulting in the Southwestern Province being defined as less similar to the other Northern Savanna zones than the Southeastern Province.

5.3.2.4. Northern Province

LOCATION AND AVIFAUNA

This province stretches from the Red Sea coast in the vicinity of Port Sudan in the east, right across the African continent between ca 8°N and 17°N to the Atlantic coast near to the mouth of the Senegal River in the west. This mainly arid province is dominated by semi-desert and *Acacia* wooded grassland, shrubland and woodland (W 43, 54a), but it is the edaphic grassland of the Niger inundation zone (W 64) that provides habitat for the province's only zone-restricted species, namely *Prinia fluviatilis*. Three species, predominantly of dry scrub, are nearly restricted to this zone, namely *Caprimulgus eximius*, *Anthoscopus punctifrons*, and *Spiloptila clamans*.

5.3.3. Southern Savanna Subregion

LOCATION AND AVIFAUNA

This subregion extends east and south of the Guineo-Congolian forests from central Kenya and the southern shores of Lake Victoria south through Tanzania, Malawi and Mozambique. From there it stretches westwards through Zimbabwe, Zambia and Angola. It is dominated by woodland and savanna, but contains important mountain blocks and coastal mosaics. It is a highly complex area in terms of topography, vegetation and avifauna. In area extent it is dominated by Zambezian woodland (66% of all one-degree grid cells that constitute the Southern Savanna Subregion). However, it is the mountain blocks of this subregion that have the highest relative species richness values (number of species per grid cell = 46.24; Table 5.3)

GENERAL POINTS

The core of this subregion, namely the Drier Zambezian Woodland, Wetter Zambezian Woodland, Zanzibar-Inhambane, Angolan Highlands and Central Tanzania Districts constitute Benson and Irwin's (1966; Table 5.4) '*Brachystegia* belt'. Forty-three of the species restricted to Southern Savanna Subregion can be considered *Brachystegia* belt endemics (labelled ^{B} in Appendix 5.1). Other species that have ranges largely centred on, but not completely restricted to, this belt do not use the *Brachystegia*

exclusively, but also use a variety of habitats found in pockets within or fringing the *Brachystegia* woodland, such forest (e.g. *Dryoscopus cubla* and *Hyliota australis*), a variety of woodlands (e.g. *Prionops retzii* and *Myrmecocihla arnotti*), *Acacia* savanna (e.g. *Tricholaema frontata* and *Lamprotornis elisabeth*), and moist grassland (e.g. *Ploceus temporalis*), or some combination thereof (e.g. *Coracias spatulata*) (labelled ^{BW} in Appendix 5.1). A few species that have ranges restricted to the geographical extent of the *Brachystegia* belt only use these habitat pockets, such as those of moist grassland (*Mirafra angolensis* and *Ortygospiza locustella*) or humid and riparian forest (e.g. *Sheppardia bocagei* and *Phylloscopus laurae*) (labelled ^{G} and ^{F} in Appendix 5.1, respectively).

Table 5.4. Benson and Irwin's (1966) geographical *Brachystegia* belt categories and corresponding Southern Savanna Subregion avifaunal districts identified by cluster and characteristic species analysis.

Benson and Irwin's (1966) geographical categories :	*Cluster districts :*
1 (Angola and southern Congo west of 22°E)	Angolan Highlands
2 (Zambia and southern Congo east of 22°E to west of the Luanga Rift, and including the Ufipa Plateau south of the Rukwa Rift)	Wetter Zambezian Woodland
3 (southwestern Tanzania, except the Ufipa Plateau)	Central Tanzania
4 (Zambia east of the Luanga Rift, Malawi and Northeastern Mozambique west of the Nyasa Rift),	Drier Zambezian Woodland
5 (Malawi and northeastern Mozambique east of the Nyasa Rift),	
6 (se Tanzania), and	
7 (Zimbabwe, including the adjoining *Brachystegia* in west central Mozambique)	
8 (southern Mozambiquan coast littoral south of 20°S)	Zanzibar-Inhambane

The *Brachystegia* avifaunal belt defined by Benson and Irwin (1966) is well recovered by the cluster analysis. The district boundaries defined by the cluster analysis that only considers nonpasserines coincide more closely with the *Brachystegia* belt subdivisions of Benson and Irwin (1966) than do those defined by the cluster analysis that is based only on passerine species distributions. As noted by Benson and Irwin (1966), the subdivisions within the *Brachystegia* belt coincide, in many instances, with the rift valleys e.g. Rukwa (e.g. *Stactolaema anchietae* and *Nectarinia oustaleti*), Ruaha (*Anthreptes anchietae*

and *Nectarinia manoensis*), and Nyasa (*Cercotrichas barbata* and *Parus griseiventris*), and the hot dry river valleys of the Zambezi (*Tockus pallidirostris* and *Nectarinia shelleyi*) and Luangwa (*Eremomela atricollis* and *Ploceus angolensis*). In a few instances these valleys separate superspecies pairs. Rukwa separates *Trocholaema* [*leucomelas*] *frontatus* and *diadematata*, as does Ruaha, while *frontatus* and *leucomelas* are separated by the Zambezi. Rukwa separates *Sylvietta* [*ruficapilla*] *ruficapilla* and *whytii*, and Luangwa separates *Phylloscopus* [*ruficapillus*] *laurae* and *ruficapillus*. Benson *et al.* (1962) suggest that such wide valleys represent an obstacle which many bird species are reticent to cross. However, a few species appear to be differentially sensitive to these dispersal barriers, failing to cross some valleys while freely crossing other valleys. In addition, instances occur where a valley may appear to prevent dispersal of one member of a superspecies pair, whereas its sister taxon freely crosses it. For instance, the distribution of *Stactolaema* [*ancheitae*] *anchietae* seems to be curtailed by Rukwa, while *whytii* appears to range across Rukwa. These valleys may not be equally effective along their entire length. For instance, *Calamonastes stierlingi* occurs mainly south of Ruaha, but continues northwards in a narrow band around the eastern (coastal) edge of the valley. Likewise, *Hyliota flavigaster* occurs mainly north of the Zambezi valley, but 'leaks' south around its mouth.

Within the *Brachystegia* belt, the Drier and Wetter Zambezian Woodland Districts cluster closely (BC = 0.213). There are four species restricted to the Drier and Wetter Zambezian Woodland grouping, all of which are inhabitants of miombo or mopane woodland (*Stactolaema whytii*, *Lybius chaplini*, *Agapornis lilianae*, and *Anthus nyassae*). However, Benson and Irwin (1966) recognised these two districts as discrete entities, and each district contains endemics, such that they are recognised in this study as two independent districts.

A number of the *Brachystegia* belt endemics show disjunct distributions. Nine occur in two disjunct populations with one in the west on the Angolan Highlands and/or escarpment, and one in the east in southeastern Democratic Republic of Congo and eastern Zambia. All of these are chiefly montane species, but they inhabit a range of habitat types, from forest (e.g. *Sheppardia bocagei*) to woodland (e.g.

Anthus caffer) and moist grassland (e.g. *Mirafra angolensis*) (Table 5.5).

Table 5.5. *Brachystegia* belt endemics that chiefly inhabit montane habitats of forest (^{F}), woodland (^{W}) or grassland (^{G}), and which have disjunct populations in the Angolan Highlands (and/or escarpment) and in the southeastern Democratic Republic of Congo and western Zambia.

Batis margaritae ^{F}, *Sheppardia bocagei* ^{F}, *Neocichla gutturalis* ^{W}, *Phylloscopus laurae* ^{F}, *Mirafra angolensis* ^{G}, *Anthreptes anchietae* ^{W}, *Nectarinia oustaleti* ^{W}, *Anthus caffer* ^{W}, and *Ploceus angolensis* ^{W}.

A number of species that occur in the eastern portion of the *Brachystegia* belt stop their westward extension short of 22°E (e.g. *Lamprotornis elisabeth*, *Calamonastes stierlingi*, and *Nectarinia shelleyi*). This coincides with the eastern border of the Angolan Highlands District identified by the cluster analysis (e.g. *Coracias spatulata* and *Serinus mennelli*). It also forms the division between Benson and Irwin's (1966) categories 2 and 1, and the eastern boundary of Hall's (1960) Angolan *Brachystegia* zone. (It is unclear what causes these species to stop their range where they do.) The western boundary of the Southern Savanna Subregion, and in particularly the *Brachystegia* belt, avifauna seems to form a gradation between 22°E and the Angolan coast. Many Southern Savanna species extend past 22°E to terminate the westward extension of their ranges on the Angolan plateau, short of the Angolan escarpment (18 species), whilst others include the escarpment in their western boundary (24 species). The Angolan escarpment runs from the mouth of the Cuanza River (9°S) to ca. the town of Benguela (13 to 15°S), separating the Angolan Highlands District and the Benguela Province. There is no difference between the variety of habitats utilized by the Southern Savanna species that extend onto the escarpment and those that stop short thereof. There is also no discernible difference between the habitat preferences of the 15 species that extend along the scarp as far south as 15°S, which is the southern escarpment border assigned by Hall (1960) and Traylor (1963; marked ^{H} in Table 5.6), and the 10 species that only extend to 13°S, which is the southern border of the escarpment assigned by the cluster analysis (marked ^{CL} in Table 5.6). Rather than being determined by the *type* of habitat, the difference may be due to the *quality* of the habitat, which decreases along the escarpment from north to south (Hall 1960; Traylor

1963). Intriguingly, a number of species only extend the western extent of their range onto the southern portion of the escarpment, avoiding the northern portion (e.g. *Falco dickinsoni*, *Corvinella melanoleuca*, and *Parus rufiventris*).

Both Hall (1960) and Traylor (1963) suggest that as the escarpment north of the Cuanza River (ca 10°S) becomes less precipitous, and the coastal plain broader, the escarpment has less effect on the distributional patterns of birds. This is born out in a number of species that have their western range boundary on the escarpment between 10 and 16°S (Table 5.6), but which extend westwards as far as the coast north of 10°S (e.g. *Anthus vaalensis*). This pattern is also seen in species that are restricted to the Benguela Province (Hall's Acacia zone) by the escarpment south of 10°S, but which occur broadly inland north of 10°S (e.g. *Bucorvus leadbeateri*).

A number of species that occur on the escarpment do not occur widely on the adjoining highland plateau. Most of these are forest, or at least forest-associated (i.e. forest edge), species (*Tockus alboterminatus*, *Batis minulla*, and *Estrilda perreini*). A few others are associated with riparian growth (*Phyllastrephus fulviventris*), rocky hillsides (*Anthus lineiventris*), or grassland (*Neolastes torquatus*). Most (five out of six) of these species extend south to between 15 and 16°S, which is suggested as the southernmost reaches of the escarpment zone by Hall (1960) and Traylor (1963), as mentioned above. Stuart *et al.* (1993) comment on the distinctness of the montane forest avifaunas of the escarpment and adjacent highlands (predominantly occurring on Mt Moco). The escarpment forest avifauna has much higher levels of endemism, with 6 out of the 12 species which they identify as montane forest species of the escarpment being endemic to the escarpment (Stuart *et al.* 1993).

The *Brachystegia* belt is bordered in the south by drier woodland types, such as mopane (*Rhinoptilus cinctus*, *Cercotrichas quadrivirgata*, and *Parus niger*), of the Zambezian Woodland-Savanna Transitional Province. In the southwest, the Zambezian Woodland-Savanna Transitional Province converges with the

Zanzibar-Inhambane District, and is then replaced by the Tonga-Pondoland Province around 24°S. The Zambezian Woodland-Savanna Transitional Province and Zanzibar-Inhambane District form the southern border of the Southern Savanna Subregion.

Table 5.6. Various patterns exhibited by species occurring on the Angolan Escarpment.

1. SPECIES WHOSE WESTWARD RANGES STOP SHORT OF THE ESCARPMENT (18 SPECIES):
Tricholaema frontata, *Caprimulgus pectoralis*, *Elminia albicauda*, *Batis molitor*, *Cercotrichas barbata*, *Parus griseiventris*, *Hirundo nigrorufa*, *Cisticola brunnescens*, *Calamonastes simplex*, *Eremomela salvadorii*, *Eremomela atricollis*, *Sylvietta ruficapilla*, *Nectarinia manoensis*, *Plocepasser rufoscapulatus*, *Ploceus temporalis*, *Euplectes progne*, *Lagonosticta nitidula*, and *Vidua obtusa*.

2. SPECIES WHOSE WESTWARD RANGES INCLUDES THE ESCARPMENT
H indicates that the species' range extends to 15°S, 13 °E as suggested by Hall (1960)(n= 15); CL indicates that the species' range extends to only 13 °S, 14 °E as suggested by the cluster analysis (n=10).

Stactolaema anchietae CL, *Campethera bennettii* H, *Merops nubicoides* H, *Lanius souzae* H, *Campephaga flava* H, *Dryoscopus cubla* H, *Tchagra anchietae* CL, *Telophorus viridis* CL, *Platysteira peltata* CL, *Monticola angolensis* H, *Turdus libonyanus* CL, *Muscicapa boehmi* H, *Myrmecocichla arnotti* H, *Lamprotornis acuticaudus* H, *Anthoscopus caroli* CL, *Parus niger* H, *Cisticola fulvicapillus* H, *Turdoides hartlaubi* H, *Pinarocorys nigricans* CL, *Anthreptes anchietae* H, *Nectarinia amethystina* H, *Petronia superciliaris* CL, *Anthus vaalensis* H, *Euplectes capensis* CL, and *Anomalospiza imberbis* CL.

3. SPECIES THAT ONLY OCCUR ONLY ON THE SOUTHERN PORTION OF THE ESCARPMENT
Francolinus sepahaena, *Glaucidium ngamiense*, *Falco dickinsoni*, *Corvinella melanoleuca*, *Prionops retzii*, *Melaenornis pammelaina*, *Parus rufiventris*, and *Motacilla capensis*.

4. SPECIES THAT RANGE STRAIGHT ACROSS THE ESCARPMENT
Lybius torquatus, *Cossypha heuglini*, *Chlorocichla flaviventris*, *Hyliota australis*, *Cisticola chinianus*, *Nectarinia bifasciata*, *Macronyx fuellebornii*, and *Euplectes orix*.

5. SPECIES THAT RANGE INTO THE COASTAL PLAIN FROM THE NORTH
Francolinus afer, *Bucorvus leadbeateri*, *Merops bullockoides*, *Caprimulgus fossii*, *Oriolus larvatus*, *Eremomela scotops*, *Turdoides jardineii*, *Mirafra africana*, *Ploceus xanthops*, *Pytilia afra*, and *Uraeginthus angolensis*.

6. SPECIES THAT OCCUR ON THE ESCARPMENT, BUT NOT WIDELY ONTO THE ADJOINING HIGHLAND PLATEAU
Tockus alboterminatus, *Batis minulla*, *Phyllastrephus fulviventris*, *Neolastes torquatus*, *Anthus lineiventris*, and *Estrilda perreini*.

The *Brachystegia* belt is bordered in the north by both drier vegetation in the form of dry grassland (e.g. *Cisticola textrix* and *C. ayresii*) and savanna (*Hirundo nigrorufa*), and by moister vegetation such as

damp grassland (e.g. *Cisticola dambo* and *Ortygospiza gabonensis*) and forest, particularly riparian types (e.g. *Phyllastrephus cabanisi*). The northwestern boundary of the Southern Savanna Subregion forms a wide transitional area that contains a high degree of species replacement (Fig. 5.5a). The forest-savanna transition between the Guineo-Congolian and Southern Savanna Subregions is gradual, taking place over a wide extent. This is in contrast to the rather abrupt forest-savanna transition between the Guineo-Congolian and Northern Savanna Subregions. Indeed, two studies recognize the avifauna of the southern forest-savanna transition to be a discrete entity (Chapin 1932; Lynes 1938). The cluster analysis suggests that the southern forest-savanna transition consists of two portions, namely the Outer and Inner Southern Congo Savanna Districts of the Southern Savanna and Guineo-Congolian Subregions respectively. A notable fact is that both of these transitional districts fall north of 10°N and therefore north of the actual Congo-Zambezi watershed divide, such that both districts fall *within* the Congo basin. Lynes (1938) gives a good description of how the vegetation changes from forest to savanna as one moves southward and upwards out of the Congo basin up to its southern rim.

Chapin (1932) identified the southern forest-savanna transitional avifauna to be one entity, *viz.* his Southern Congo Savanna District (no. 5). However, Lynes (1938) divided it into three zones, namely the Inner, Transitional, and Outer Basin zones. Together the Inner and Outer Southern Congo Savanna zones (of the Guineo-Congolian and Southern Savanna Subregions, respectively) identified by the cluster analysis correspond to the extent of Chapin's Southern Congo Savanna District. The Inner Southern Congo Savanna District (of the Guineo-Congolian Subregion) coincides well with Lynes' (1938) Inner (Congo) Basin zone, and the Outer Southern Congo Savanna Province (of the Southern Savanna Subregion) corresponds with his Transitional zone. Lynes' (1938) Outer (Congo) Basin zone falls across the northern extents of our Wetter Zambezian Woodland and Angolan Highlands Districts, such that Lynes' total forest-savanna transition is broader than that identified by Chapin (1932) or the cluster analysis.

Lynes (1938) does not attempt to explain the cause of the differences observed between his zones other

than to comment that the avifauna of the Inner zone is predominated by forest birds, while that of the Outer zone is predominated by woodland birds. Lynes suggested that this is simply due to the occurrence of available habitat. The Guineo-Congolian Subregion species probably play a larger role in defining the boundaries of the individual districts that make up the southern forest-savanna transition than do the Southern Savanna Subregion species. Working from south to north, the western portion of the Outer Southern Congo Savanna Province is essentially defined by forest species of lowland and montane forms that extend from the main Guineo-Congolian forest block. Such species sometimes occur broadly into northern Angola and the adjacent coast (e.g. *Neocossyphus poensis*, *Sylvietta virens*, and *Nectarinia superba*; marked ^{B} in Table 5.7), or show a narrow continuation between the main forest block and forest areas of northern Angola (e.g. *Trochocercus nitens*, *Eremomela badiceps*, and *Nectarinia chloropygia*; marked ^{J} in Table 5.7). Other species are often represented only by a disjunct population in Cuanza Norte of Angola, occasionally including adjoining portions of Malanje and/or Luanda (e.g. *Ceratogymna atrata*, *Macrosphenus flavicans*, and *Nigrita bicolor*; marked ^{CN} in Table 5.7), or by a disjunct population which extends to various degrees along the escarpment (e.g. *Gymnobucco calvus*; marked ^{ES} in Table 5.7). Some of the species showing a disjunct population within this district, whether restricted to Cuanza Norte or extending into the escarpment, occur fairly widely within the Congo basin (e.g. *Spizaetus africanus*, *Oriolus brachyrhynchus*, and *Illadopsis fulvescens*). However, other species showing a disjunct population within this district occur in localized areas either restricted to the Lower Guinea, in the Cameroon-Bameda Highlands and adjoining lowlands, the mountains around Lake Victoria, and northern Angola (e.g. *Apalis binotata*), or occur in localized areas throughout the Guineo-Congolian Subregion, stretching from the Upper Guinea to Cameroon-Bameda Highland adjoining lowlands, Albertine Rift area, and northern Angola (e.g. *Telophosrus multicolor*). Some, whether occurring broadly within the basin or not, show an additional disjunct population on the Angola-Zambia border (e.g. *Columba unicincta*) or southern Eastern Arc Mountains (e.g. *Illadopsis rufipennis*). One species, *Anthus pallidiventris*, showing a disjunct distribution, is a dry grassland species occurring in the west of the basin with a disjunct population in the valley of the lower Cuanza River in Angola.

Forest species are known to extend their distributional ranges into savanna biotopes along the gallery forest of rivers. A number of Guineo-Congolian species extend into the Outer Southern Congo Savanna Province roughly between 18°E and 24°E. Five forest species that extend into the Outer Southern Congo Savanna Province in a narrow band between 20°E and 22°E (*Dryoscopus senegalensis*, *Laniarius lecuorhynchus*, *Andropadus gracilis*, *Macrosphenus concolor*, and *Nectarinia johannae*) may indicate the role of sampling bias along an access route that falls directly in this band (used by Lynes and Vincent 1933-34) in this observation. However, this region is traversed by numerous rivers, some of which incise the highlands (1000-1500 m) of Lunda (Angola) and Katanga (Democratic Republic of Congo). *Sylvietta denti* occurs in the northern reaches of the Congo basin, but reappears in this band in a isolated population. *Anthreptes rectirostris* extends south to the same extent as the aforementioned species, but rather between 22°E and 24°E, being absent between 18°E and 20°E. Four species (*Tricholaema hirsuta*, *Alethe diademata*, *Alethe castanea*, and *Criniger calurus*) extend south to the same extent (8°S to 10°S) between 20°E and 24°E. One species extends south between 16°E and 18°E, namely *Tauraco schuetti*. Most of the species discussed in this section are forest species, with only a few using forest clearing or edge habitat. There is no differentiation in habitat use between these subcategories, which may suggest that we do not perceive available vegetation as do birds.

Seven forest species of the Guineo-Congolian Subregion occur broadly into the Outer Southern Congo Savanna Province. Although none of them really define the southern boundary thereof (*Pogoniulus scolopaceus*, *Prodotiscus insignis*, *Campethera nivosa*, *Accipiter castanilius*, *Bleda syndactyla*, *Ploceus nigricollis*, and *Spermophaga haematina*), they will highlight the difference between the avifaunas of the Outer Southern Congo Savanna Province and those districts to the south thereof that fall within the *Brachystegia* belt.

Looking now at the Inner Southern Congo Savanna District, four forest species define the southern border of this district well (*Pogoniulus subsulphureus*, *Buccanodon duchaillui*, *Urotriorchis macrourus*, and *Thescelocichla leucopleura*). A number of others do so in a less well defined manner (e.g.

Pogoniulus atroflavus, *Muscicapa olivascens*, and *Ixonotus guttatus*). Other forest species that extend into this district do so only in a patchy manner (e.g. *Merops muelleri*, *Dryoscopus sabini*, *Cisticola anonymus*, and *Malimbus erythrogaster*), or only in the western portion thereof (e.g. *Caprimulgus batesi*), and probably do not help to define the district, but rather establish its affinity with the Guineo-Congolian Subregion. Some of the forest species that extend into the Inner Southern Congo Savanna District do so only in the area underlain by Kalahari sand (e.g. *Phoeniculus castaneiceps*, *Merops breweri*, *Glaucidium tephronotum*, and *Pitta reichenowi*), [see Table 5.7 under the heading of 'forest species extending into the Inner Southern Congo Savanna District' for a full listing of all species showing patterns discussed in this paragraph].

Species characteristic of the Southern Savanna Subregion play some role in defining these two districts. Southern Savanna Subregion species of *Brachystegia* woodland (e.g. *Tricholaema frontata*, *Prodotiscus zambesiae*, and *Plocepasser rufoscapulatus*), forest (e.g. *Merops boehmi*, *Sheppardia bocagei*, and *Phylloscopus laurae*), and riparian vegetation (e.g. *Glaucidium ngamiense* and *Hypargos niveoguttatus*), occur up to the southern boundary of the Outer Southern Congo Savanna Province. Woodland and savanna species such as *Oriolus larvatus*, *Turdus libonyanus*, and *Parus griseiventris* define the northern border of the Outer Southern Congo Savanna Province and of the Southern Savanna Subregion, while a number occur only patchily into this district supporting its affinity to the Southern Savanna Subregion (e.g. *Falco dickinsoni*, *Monticola angolensis*, and *Hirundo nigrorufa*).

A number of predominantly Southern Savanna Subregion species, with a range of habitat preferences (e.g. *Cossypha natalensis*, *Dryoscopus cubla*, and *Turdoides jardineii*), occur up to the northern border of the Inner Southern Congo Savanna District, defining it well (Table 5.7). Others extend more patchily into this district (e.g. *Ceratogymna bucinator*, *Parus leucomelas*, and *Cisticola lepe*), particularly along the area underlain by Kalahari sands (see van Zinderen Bakker 1976; Hamilton 1982 for discussion) (e.g. *Batis molitor*, *Sylvietta ruficapilla*, and *Petronia superciliaris*). Some of these species also extend into the neighbouring Guineo-Congolian Subregion zones of the Gabon District (e.g. *Lybius minor*, *Ploceus*

Table 5.7. Various species patterns of the southern forest-savanna transition

1. SOUTHERN SAVANNA SUBREGION SPECIES RANGING INTO THE OUTER CONGO SAVANNA DISTRICT. (N=9)

Lybius torquatus, *Campethera bennettii*, *Falco dickinsoni*, *Oriolus larvatus*, *Monticola angolensis*, *Turdus libonyanus*, *Myrmecocichla arnotti*, *Parus griseiventris*, and *Hirundo nigrorufa*.

2. SOUTHERN SAVANNA SUBREGION SPECIES RANGING INTO THE INNER SOUTHERN CONGO SAVANNA DISTRICT. (N=29)

Francolinus afer, *Stactolaema anchietae*, *Lybius minor*, *Ceratogymna bucinator*, *Coracias caudata*, *Merops bullockoides*, *Merops nubicoides*, *Lanius souzae*, *Campephaga flava*, *Elminia albicauda*, *Dryoscopus cubla*, *Batis molitor*, *Melaenornis pammelaina*, *Cossypha natalensis*, *Anthoscopus caroli*, *Parus leucomelas*, *Cisticola lepe*, *Cisticola dambo*, *Calamonastes simplex*, *Eremomela scotops*, *Sylvietta ruficapilla*, *Turdoides jardineii*, *Nectarinia amethystina*, *Petronia superciliaris*, *Ploceus xanthops*, *Euplectes progne*, *Pytilia afra*, *Uraeginthus angolensis*, and *Ortygospiza gabonensis*.

3. GUINEO-CONGOLIAN SUBREGION SPECIES RANGING INTO THE OUTER SOUTHERN CONGO SAVANNA DISTRICT. (N= 80)

^{CN} = Disjunct population restricted to Cuanza Norte, and occasionally the adjoining areas of Malanje and Luanda (n=28), ^{ES} = those stretching along the escarpment (n=13), ^{J} = those species showing a small connection to the main forest block (n=8), and ^{B} = those occurring broadly into northern Angola (n= 11).

Gymnobucco calvus ^{ES}, *Pogoniulus scolopaceus*, *Tricholaema hirsuta*, *Trachyphonus purpuratus* ^{B}, *Prodotiscus insignis*, *Sasia africana* ^{B}, *Campethera nivosa*, *Dendropicos xantholophus* ^{B}, *Ceratogymna fistulator* ^{B}, *Ceratogymna atrata* ^{CN}, *Merops gularis* ^{CN}, *Centropus anselli* ^{CN}, *Poicephalus gulielmi* ^{CN}, *Tauraco schuetti*, *Corythaeola cristata* ^{ES}, *Columba unicincta* ^{CN}, *Columba iriditorques* ^{CN}, *Dryotriorchis spectabilis* ^{B}, *Accipiter castanilius*, *Spizaetus africanus* ^{CN}, *Oriolus brachyrhynchus* ^{CN}, *Dicrurus modestus* ^{CN}, *Trochocercus nitens* ^{J}, *Terpsiphone rufocinerea* ^{J}, *Dryoscopus senegalensis*, *Laniarius leucorhynchus*, *Telophorus bocagei* ^{CN}, *Telophorus multicolor* ^{ES}, *Bias flammulatus* ^{CN}, *Bias musicus* ^{J}, *Platysteira castanea* ^{ES}, *Platysteira concreta* ^{ES}, *Neocossyphus poensis* ^{B}, *Alethe poliocephala* ^{ES}, *Alethe diademata*, *Alethe castanea*, *Muscicapa comitata* ^{B}, *Myioparus griseigularis* ^{CN}, *Cercotrichas leucosticta* ^{ES}, *Poeoptera lugubris* ^{CN}, *Onychognathus fulgidus* ^{CN}, *Pholidornis rushiae* ^{CN}, *Parus funereus* ^{ES}, *Andropadus gracilis*, *Andropadus curvirostris* ^{CN}, *Andropadus latirostris* ^{ES}, *Phyllastrephus albigularis* ^{ES}, *Bleda syndactyla*, *Criniger calurus*, *Prinia bairdii* ^{CN}, *Apalis jacksoni* ^{CN}, *Apalis binotata* ^{CN}, *Apalis rufogularis* ^{ES}, *Camaroptera superciliaris* ^{CN}, *Eremomela badiceps* ^{J}, *Sylvietta virens* ^{B}, *Sylvietta denti*, *Macrosphenus flavicans* ^{CN}, *Macrosphenus concolor*, *Hylia prasina* ^{ES}, *Illadopsis albipectus* ^{CN}, *Illadopsis rufipennis* ^{CN}, *Illadopsis fulvescens* ^{ES}, *Anthreptes fraseri* ^{CN}, *Anthreptes rectirostris*, *Nectarinia seimundi* ^{B}, *Nectarinia chloropygia* ^{J}, *Nectarinia johannae*, *Nectarinia superba* ^{B}, *Anthus pallidiventris*, *Ploceus nigricollis*, *Ploceus nigerrimus* ^{J}, *Ploceus tricolor* ^{CN}, *Malimbus malimbicus* ^{J}, *Parmoptila woodhousei* ^{CN}, *Nigrita fusconota* ^{CN}, *Nigrita bicolor* ^{CN}, *Nigrita luteifrons* ^{B}, *Nigrita canicapilla* ^{J}, and *Spermophaga haematina*.

4. GUINEO-CONGOLIAN SUBREGION SPECIES RANGING INTO THE INNER SOUTHERN CONGO SAVANNA DISTRICT. (n = 45)

Francolinus lathami, *Pogoniulus atroflavus*, *Pogoniulus subsulphureus*, *Buccanodon duchaillui*, *Indicator maculatus*, *Phoeniculus castaneiceps*, *Tockus albocristatus*, *Tockus hartlaubi*, *Tockus camurus*, *Ceratogymna albotibialis*, *Apaloderma aequatoriale*, *Merops muelleri*, *Merops breweri*, *Merops malimbicus*, *Ispidina lecontei*, *Halcyon badia*, *Centropus leucogaster*, *Cercococcyx mechowi*, *Chrysococcyx flavigularis*, *Psittacus erithacus*, *Agapornis swindernianus*, *Bubo poensis*, *Jubula lettii*, *Glaucidium tephronotum*, *Caprimulgus batesi*, *Urotriorchis macrourus*, *Pitta reichenowi*, *Smithornis rufolateralis*, *Coracina azurea*, *Erythrocercus mccallii*, *Trochocercus nigromitratus*, *Dryoscopus sabini*, *Fraseria ocreata*, *Fraseria cinerascens*, *Muscicapa olivascens*, *Lamprotornis purpureiceps*, *Ixonotus guttatus*, *Thescelocichla leucopleura*, *Phyllastrephus icterinus*, *Bleda eximia*, *Cisticola anonymus*, *Camaroptera chloronota*, *Eremomela turneri*, *Nectarinia minulla*, and *Malimbus erythrogaster*.

xanthops, and *Uraeginthus angolensis*) and/or the Albertine Rift Province (e.g. *Merops bullockoides*, *Anthoscopus caroli*, and *Ortygospiza gabonensis*). Three species are essentially restricted to the united area of the Inner and Outer Southern Congo Savanna Provinces, two of forest, namely *Tauraco erythrolophus* and *Batis minulla*, and the grassland savanna species, *Neolestes torquatus*.

5.3.3.1.1. Drier Zambezian Woodland District

LOCATION AND AVIFAUNA

Centred on the dry Zambezi River valley, this district stretches from around 36°E to the Victoria falls in the west, from Lake Nyasa (Malawi) in the north to the Kruger National Park (South Africa) in the south. It consists mainly of a variety of woodlands, each with its associated zone-restricted species, including *Dendropicos stierlingi* of the *Brachystegia* dominated miombo (W 26) and *Agapornis nigrigenis* of the mopane (W 28). There are a number of important montane blocks such as the Chimanimani and Inyanga Mountains of eastern Zimbabwe, which support montane forest species (*Alethe choloensis*, *Andropadus milanjensis*, and *Apalis chirindensis*) and specialists of heath and bracken (*Oreophilias robertsi*).

GENERAL POINTS

It is interesting to note that this district extends to the Indian ocean coastline between the Zambezi River mouth and the town of Beira (Mozambique). This result is verified by Irwin's (1963) observation that the avifauna of this area is typical of the plateau *Brachystegia*, and so of greater affinity with the southern Zimbabwe highlands than the adjacent coastal lowlands. This situation probably results from an eastward extension of the highlands in this region, in the form of the Gorongosa massif. In addition, the Gorongosa massif, together with a patch of open 'tandos' grass and drier *Brachystegia* woodland, limits the westward expansion of 'coastal' (i.e. assume coastal forest) avifauna (Irwin 1963). Consequently it is not surprising that these coastal grid cells cluster with those of the Drier Zambezian Woodland District rather than those of the Zanzibar-Inhambane District which flank the coastal grid cells under discussion to the north and south.

5.3.3.1.2. Wetter Zambezian Woodland District

LOCATION AND AVIFAUNA

This district coincides with the greater part of Zambia from the Malawi border in the east to the Angolan border in the west, stretching from the southeastern mountains of the Democratic Republic of Congo (Mts Malimba, Marunga, Hakansson, Kundelungu and Mugila) to 16°S. The predominantly moist climate of this district is reflected in the moist miombo (W 25), edaphic grassland (W 60, 64), and swamp (W 75) vegetation. Although the forests found in this district are classified as dry evergreen forest (W 6), the forest bird species restricted to this district inhabit humid forest (*Tauraco livingstonii*). The remaining three zone-restricted species are swamp specialists, namely *Ploceus katanga*, *P. ruweti*, and *Estrilda nigriloris*.

5.3.3.1.3. Zanzibar-Inhambane District

LOCATION AND AVIFAUNA

This district stretches along the East African coast from Dar es Salaam (Tanzania) to Maputo (Mozambique). It essentially consists of a coastal mosaic (W 16a), with patches of forest (W 16b) and mangrove (W 77), interdigitated with miombo (W 25, 26) and mopane (W28) woodlands that intrude from the west. This mix of forest and woodland is well demonstrated by the habitat preferences of the characteristic species *Batis soror*. Zone-restricted species utilize coastal forest habitats (*Pogoniulus simplex*, *Batis reichenowi*, and *Macrosphenus kretschmeri*), sand forest and thornveld (*Nectarinia neergaardi*), and Palm savanna and adjacent *Acacia* savanna (*Serinus citrnipectus*).

5.3.3.1.4. Angolan Highlands District

LOCATION AND AVIFAUNA

Centred on the Bie Plateau of central Angola, the Angolan Highlands District extends from 22°E to 15°E and from 9°S to 16°S. It encompasses a large patch of Wetter Zambezian miombo (W 25) that is separated from the more easterly block Wetter Zambezian miombo (which falls largely within the Wetter Zambezian Woodland District) by an intrusion of edaphic and secondary grassland on Kalahari sand (W 60) from the south.

GENERAL POINTS

Two mountains, Mt Soque and Moco, fall within the geographical extent of this district. However, the species endemic to the montane forest patches that occur on these peaks are considered relicts (Hall 1960; Stuart *et al.* 1993). As the closest relatives of these species inhabit the isolated mountain peaks fringing the Congo basin (Hall 1960; Stuart *et al.* 1993), the avifauna of these mountains are probably best considered to be part of the Guineo-Congolian Subregion. An example is *Francolinus* [*camerunensis*] *swierstrai*, which occurs in the montane forest of Angola. It forms a superspecies with *Francolinus* [*camerunensis*] *camerunensis*, which species is restricted to Mt Cameroon. This pattern is also seen in species of highland woodland (*Nectarinia* [*tacazze*] *bocagii*), whose closest relatives occur on the mountains of the Albertine Rift, (*N.* [*tacazze*] *purpureiventris*) and other east African mountains (*N.* [*tacazze*] *tacazze*).

Interestingly, the separation of the miombo block that occurs in the Angolan Highlands from the larger eastern miombo block by grassland has not resulted in much speciation of the woodland birds of the Angolan Highlands. Possibly the miombo patch is too large to allow for random genetic drift, founder effect, and other genetic mechanisms which often lead to differentiation in isolated populations (e.g. Stansfield 1983) to have taken effect. It is also quite probable that the isolation of the miombo avifauna is not complete, allowing gene flow with the larger populations of the eastern miombo block.

5.3.3.1.5. Central Tanzania District

LOCATION AND AVIFAUNA

This district stretches from 35°E to Lake Tanganyika in the west, from the southern shores of Lake Victoria to Lake Rukwa (8°S) in the south. It consists mostly of lowland, except for the Mugila (or Marunga *sensu* Stuart *et al.* 1993) mountain. Forested mountains in southeast of the Democratic Republic of Congo host one of the four zone-restricted species, *Apalis kaboboensis*. Dry woodland (W 26), bushland and thickets (W 42, 35a, 40) (*Francolinus rufopictus* and *Histurgops ruficauda*), and semi-aquatic vegetation (W 64) (*Ploceus reichardi*) also occur.

5.3.3.2. Eastern Arc Province

LOCATION AND AVIFAUNA

This district maps, almost exactly, the central and southern Kenyan mountains (the Aberdares and Mt Kenya), the northern Tanzanian mountains (Kilimanjaro), the Eastern Arc Mountains (the Taita Hills, North and South Pares, East and West Usambaras, Nguu, Nguru, Ukaguru, Rubeho (Usaguru), Uluguru, Malundwe, Mahenge, and Uzungwas; *sensu* Lovett 1988), and the southern Tanzanian mountains (Kipengere, Mbeya, Poroto, Rungwe, and Livingstone). Although in area extent this district is dominated by the Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (W 42), which stretches north-eastwards into the Horn of Africa Province of the Northern Arid Subregion, only two of this district's 34 zone-restricted species inhabit the *Acacia* savanna (*Lamprotornis hildebrandti* and *Cosmopsarus unicolor*). The majority of the zone-restricted species are montane forms of forest (*Laniarius fuelleborni, Sheppardia sharpei, S. montana, S. lowei, Poeoptera kenricki, Cinnyricinclus femoralis, Andropadus masukuensis, A. nigriceps*, and *Modulatrix stictigula*), or forest associated habitats such as forest clearings (*Cisticola hunteri*) and forest edges (*Turdoides hypoleucus*), and of nonforest habitats such as bracken (*Cisticola njombe*) and grasslands (*Euplectes jacksoni*). Many of the montane species are endemic to a single or a few particular mountains, for example Aberdares (*Cisticola aberdare*), Ulugurus (*Malaconotus alius* and *Nectarinia loveridgei*), Uzungwas (*Xenoperdix udzungwensis* and *Nectarinia rufipennis*), and Kipengere (*Serinus melanochrous*). These mountains are embedded in a mixture of drier Zambezian miombo woodland (W 26) to the west and Zanzibar-Inhambane East African coastal mosaic (W 16a) to the east (see Wasser & Lovett 1993 for a description). The coastal lowland forests (*Otus ireneae* and *Ploceus golandi*), particularly the Arabuko-Sokoke, are also important in determining the diversity and uniqueness of the avifauna of this district.

The large number of passerines endemic to the Eastern Arc Mountains has led to this district being defined as the geographical extent of the Eastern Arc Mountains. The number of nonpasserine species restricted to the eastern Arc mountains is relatively few, so that the pattern of the *Acacia* savanna species which extend into the Ethiopian Rift (e.g. *Pterocles gutteralis* and *Nectarinia mariquensis*) predominate

when nonpasserines alone are considered. This results in the nonpasserines defining a much broader zone in the same geographical area as the Eastern Arc Province, and the nonpasserines identify this zone as closely related to the Ethiopian Highlands. This situation highlights a problem common in such broad scale analysis, which cannot differentiate between altitudinal differences experienced in the same, limited geographical area.

5.3.3.3. Zambezian Woodland-Savanna Transitional Province

LOCATION AND AVIFAUNA

Running southeast from southern Angola, across northern Botswana and southern Zimbabwe to just north of the Limpopo, this is a truly transitional province both in terms of vegetation and lack of a diagnostic bird fauna. Although it incorporates the Okavango swamp (W 28), the exclusion of waterbirds from this analysis results in the importance of the Okavango for waterbird life not being reflected here.

GENERAL POINTS

This transitional zone between the avifauna of the more mesic central highlands and arid southwest is also recognised by Winterbottom (1978). However, Winterbottom (1978) included the Angolan Escarpment in this transitional zone, which the cluster analysis, Hall (1960), and Traylor (1963) suggest is more closely affiliated with the Guineo-Congolian forest avifauna (rather than with that of the Zambezian woodland-savanna transition). Winterbottom (1978) suggested that *Tockus bradfieldi* and *Agapornis nigrigenis* are largely confined to this transition zone. However, more recent data show that *Tockus bradfieldi* is only 56 % restricted to the Zambezian Woodland-Savanna Tansitional Province, and only a small part of the range of *Agapornis nigrigenis* falls within this district, so that the tally of species endemic to this district remains zero.

5.3.3.4. Outer Southern Congo Savanna Province

LOCATION AND AVIFAUNA

This province stretches along the scarp of the southern Congo basin from the Angolan (Cuanza Sul) escarpment to just west of Lake Tanganyika. It is dominated by a mosaic of lowland rain forest and

secondary grassland (W 11a). All seven of its zone-restricted species are restricted to the forest patches of Angola. It coincides with the southern portion of Chapin's (1932) Southern Congolian Savanna Subregion. It forms part of a broad forest-savanna transition (see discussion above under 'General Points' of the Southern Savanna Subregion).

5.3.3.5. Tongaland-Pondoland Province

LOCATION AND AVIFAUNA

This zone essentially comprises the southeastern coast of South Africa from Lake Kosi in the north to Algoa Bay in the south, and westwards inland to the southern slopes of the Drakensberg Mountains. There is a northward protrusion west of the Kruger National Park as far as Tzaneen (24°S, 3°E), possibly attributable to evergreen forest species (see Clancey 1986). The vegetation of this district is dominated by coastal mosaic (W 16c) and various woodland types (W 48, 29d, 24). Some of the zone-restricted species utilize either the coastal lowland (*Cercotrichas signata*) or montane (*Monticola pretoriae* and *Promerops gurneyi*) habitats exclusively, whilst others range from the lowlands into the mountains (e.g. *Cossypha dichroa*). Four of the six zone-restricted species are forest species, namely *Cossypha dichroa, Cercotrichas signata, Bradypterus barratti*, and *Lioptilus nigricapillus*. *Monticola pretoriae* inhabits rocky montane areas and cliffs, while *Promerops gurneyi* uses montane proteas and aloes.

5.3.3.6. Benguela Province

LOCATION AND AVIFAUNA

This province represents the thin coastal strip west of the Angolan Escarpment from the mouth of the Cuanza River (9°S) to Benguela (ca. 12°S). It consists of dry coastal grassland with scattered *Acacia* utilized by its two zone-restricted species *Euplectes aureus* and *Mirafra naevia*.

GENERAL POINTS

The Benguela Province as identified by the cluster analysis only encompasses the northern portion of Hall's (1960) and Traylor's (1963) Angolan *Acacia* zone. It does not include the southerly portion of their zone, which stretches as far south as Moquamedes at around 15°S, as this portion covers the Namib

desert and semi-desert thornveld tongues which extend from the south and are defined as part of the Kalahari Province of the Southwestern Subregion by the cluster analysis.

5.3.4. Guineo-Congolian Subregion

LOCATION AND AVIFAUNA

The forest that occurs to the north of the Southern Savanna Subregion dominates central and western Africa, stretching from 36°E to central Sierra Leone (14°W), and from around 9°N to around 6°S. The Guineo-Congolian Subregion (spelling *sensu* White 1983), as defined by the cluster analysis, encompasses all of the Guineo-Congolian lowland and montane forest of West and Central Africa, as well as the Lake Victoria mosaic (W XII) of East Africa This is one of the most strongly defined subregions at a BC = 0.45, with 30 characteristic species and 121 zone-endemic species.

GENERAL POINTS

Although in comparison with other tropical forest the flora of the Guinea-Congo is relatively depauparate and has many widespread elements (see Richard's "Odd man out" hypothesis, 1973), the mosaic nature of this forest expanse - largely due to the interdigitation of humid (W 1a), swamp (W 8), and riverine forest with drier forest types (W 2), including isolated montane pockets - has lead to an intricate pattern of avifaunal zones. This has resulted in the identification of nine subdivisions, seven of which constitute lowland forest, and two of which are identified largely from their montane elements, namely the Mt Cameroon District and the Albertine Rift Province. The lowland subdivisions fall chiefly into the Guinean and Congolian Provinces, which form the primary division in this subregion, with the Ubangi-Uelle Savanna and Albertine Rift Provinces being somewhat peripheral to the main block of Guineo-Congolian forest. Failure of the Crowe and Crowe (1982) scheme to identify the mountain entities as distinct zones results from the coarser scale employed in their study.

A number of the Guineo-Congolian avifaunal elements extend to varying degrees into the neighbouring savanna subregions along wooded river valleys and into outlying forest patches. The transition from

forest to savanna is sharp to the north of the Congo basin, taking place over a short distance as shown by the identification of the narrow Ubangi-Uelle Savanna Province. Although in Chapin's (1932:85) text he comments on the sharpness of this transition, he defines his Ubangi-Uelle Savanna Province as somewhat wider than is suggested by the cluster analysis. A narrower definition is supported by a tight band of species replacement (Fig. 5.5a). The forest-savanna transition north of the Guinea forest block is more complex. Chapin (1932) defines it as the Upper Guinea Savanna District within his forest (West African) subregion. The cluster analysis identifies the area as more closely related to the Northern Savanna Subregion in the form of the Southwestern Province. It is represented by a tight band of species range-edges (Williams *et al.* in press), although the band of species replacement is somewhat wider. This is probably due to the intricate interdigitation of true forest vegetation with a band of forest transition and secondary grassland mosaic (W 11a), which is almost as wide as the strip of Guinea forest. The situation is also complicated by a number of small mountain blocks (e.g. Mt Nimba and Mt Macenta). All these vegetation elements occurring in such close proximity lead to repeated replacement of highland and lowland, forest and nonforest avifaunal elements over short distances and the resultant complex pattern of species replacement indicated in Fig. 5.5a. The southern forest-savanna transition is much more gradual, taking place over a wide geographical extent (as discussed above under the Southern Savanna Subregion). The eastern border of the Guineo-Congolian Subregion cannot be viewed as straight forest-savanna transition, occurring as it does in an area of complex topography. The mountains of the Albertine Rift represent a 'melting pot' where a number of avifaunas meet (Fanshawe & Bennun 1991), including those of lowland and montane forest and northern and southern savanna. For instance, the lowland forest of Ituri extends eastward between Lendu Plateau and the Ruwenzori Mountains, and along Lake Albert, to numerous patches west and north of Lake Victoria and to Kakamega Forest (Kenya). This area roughly corresponds to Chapin's (1932) Uganda-Unyoro Savanna District. The highland forest extends in a more north-south direction from the mountains of the Nile headwaters along the chain of mountains on the western side of the Albertine Rift. This situation again emphasises the inability of a study conducted at the scale of this one to separate out altitudinal zones that replace each other over short distances, resulting in complex situations (as discussed above under the Southern Savanna Subregion).

Opinions on the subdivision and nomenclature for the resultant biogeographical zones of the Guineo-Congolian forests vary. Reichenow's study on African birds (1886 cited Chapin 1932:85) identified a single dichotomy situated in the vicinity of Mt Cameroon and the Bameda Highlands, resulting in an Upper Guinea, *sensu lato*, constituting the forests of West Africa (including Nigeria), and a Lower Guinea, constituting the forests of Central Africa This arrangement is congruent with that of Udvardy's (1975:6) Guinean and Congo rainforest Provinces (based on the flora and fauna of the world), Crowe and Crowe's (1982) Western Forest District and Eastern Forest Province (based on terrestrial Afrotropical birds), and Louette's (1992) Upper and Lower Guinea (based on stenotypic forest bird species). Chapin (1932, based on African birds) also recognized two major entities, but include the Nigerian forests with those of the central forest, as did Moreau (1969: west African forest vertebrates) and Mayr and O'Hara (1986: Afrotropical forest refugia). These latter arrangements resulted in the Dahomey Gap, first noted by Sharpe (1893 cited by Chapin 1932), being identified as the major forest division. The Dahomey Gap is a savanna mosaic with patches of forest (Keay 1959) that reaches the coast of West Africa at Togo and Benin, breaking the forest over a width of about 250km (Diamond & Hamilton 1980)

Jenkins (1992, based on phytogeography) and Lowe (1992) would seem to support the view that the primary forest subdivision occurs at the Dahomey Gap as they suggest that the Nigerian forest is most closely allied with the Lower Guinea. However, both authors, although they recognize the largely transitional nature of the Nigerian forest, identify the Nigerian forests as an entity distinct from either the West or Central African forests. This pattern is followed by a number of authors (e.g. Moreau 1966; Brenan 1978; Lawson 1996), who consequently recognize three distinct lowland forest entities, namely the Upper Guinea, *sensu stricto*, (Moreau 1966; Lawson 1996) or West African rainforest (Brenan 1978; Jenkins 1992); the Nigerian rainforest (Brenan 1978), Lower Guinea (Lawson 1996) or transitional zone (Jenkins 1992); and the Central African rain forest (Brenan 1978), Congolean rain forest (Jenkins 1992), or Congolia (Lawson 1966). The cluster analysis supports the recognition of these three entities as the Upper Guinea and Lower Guinea Districts, which together form the Guinean Province, and a Congolian Province. The Congolian Province consists of the Central, Disjunct, Gabon, Mt Cameroon, and Inner

Southern Congo Savanna Districts.

The definition of the borders of the Lower Guinea (or Nigerian forest) is a matter of some dispute. All previous studies agree that its western border is the Dahomey Gap, but the eastern border is placed variably at the Cameroon Highlands (Moreau 1966: birds), the Cross River (Brenan 1978: phytogeography; Jenkins 1992: a number of taxa particularly amphibians and mammals, our cluster analysis), and even as far south as the Sanaga River in Cameroon (Lawson 1996: vascular plants). The identification of a 'suture line' (*sensu* Louette 1992:214) in Nigeria is complicated by a number of extant and historical features, such as current differences in the physical environment experienced in various portions of the Nigerian forests as well as historical savanna intrusions and the action of rivers as barriers to dispersal (see detail below). These factors combine to result in the division of the Nigerian forest into three entities, namely the eastern forest east of the Cross River, the central forest between the Cross and Niger Rivers, and the western forest between the Niger River and the Dahomey Gap (e.g. Rosevear 1953: mammals; Hall 1977: forest trees). There are also differences in the geology. For example, the soils of the western entity are less well drained, at least seasonally, as compared to those of the central entity, with differences in the soil possibly reflecting differences in the parent rock material (Hall 1977). The avifaunal relationships between the three Nigerian forest entities are not simple, with the birds showing a number of varied patterns demonstrating every possible combination of the three entities. Two Guineo-Congolian species occur only in western Nigeria, being absent from both central and eastern Nigeria, although one of these, namely *Francolinus* [*squamatus*] *ahantensis*, is replaced by a congener, namely *F.* [*squamatus*] *squamatus*, on the eastern side of the Niger River. In this case the Niger River, which is roughly a mile wide [1.6km] at the inland boundary of the forest (Rosevear 1953), is likely to have acted as a physical dispersal barrier to the terrestrial and rather sedentary francolin, allowing differentiation of the populations either side of the river to superspecies level. (Note that Moreau (1969) puts the river at only a few hundred yards wide, but the account of Rosevear who worked in Nigeria for a number of years is likely to be more accurate.) Other species occur in western and eastern Nigeria but are absent in the central forests (e.g. *Campethera caroli* and *Coracina azurea*). A number of studies refer to the high

human impact between the Niger and Cross Rivers, which may eradicate the species or their habitat (e.g. Rosevear 1953). An apparent phytogeographical discontinuity somewhere between the Cross and Niger Rivers was noted by Brenan (1978). The agricultural activity of this area, which is of ancient origin, takes the form of yams and cassava, which demand clear felling and result in permanent deforestation (Rosevear 1956:17), such that one might expect such discontinuities to be of purely anthropogenic origin. A number of species occur only in eastern Nigeria, being absent in both western and central Nigeria. Many of these are Congolian species, which reach the western boundary of their distributions in the vicinity of the Cross River (e.g. *Gymnobucco bonapartei* and *Smithornis sharpei*). Western and central Nigeria experience a desiccating northeasterly harmattan wind during the dry season (White 1983), which is noted to reduce the relative humidity to 40 % at 13h00 local time in Nigeria (Rosevear 1953). The harmattan winds also affect relative humidity in Ghana where it drops to 53 % at 15h00 GMT (White 1983). Orographic rainfall due to maritime air being forced to rise by the Cameroon Highlands results in a wetter climate in the eastern Nigerian forest (Hall 1977). It is fairly widely believed that the distribution of Guineo-Congolian forest plant species is related to a combination of the amount and evenness of rainfall, relative humidity, soil moisture (White 1983:74; Rosevear 1953:14), and soil composition (Hall 1977), such that one may expect some difference in the Nigerian forests west and east of the Cross River purely due to extant environmental differences. Indeed, this may explain Brenan's (1978) observation that 73 of the plant genera occurring in the Upper Guinea west of the Dahomey Gap do not occur in west and central Nigeria, only reappearing in east Nigeria (or countries even more easterly or southerly). A combination of extant differences in floral and environmental composition in the Nigerian forest west of the Cross River could be expected to result in stenotypic species curtailing their ranges east of the Cross River without having to postulate the action of the river as an insurmountable physical obstacle. In addition, it is postulated that the Nigerian savanna would have reached as far south as the coast west of the Cross River intermittently during dry climatic phases (Hall 1977; Lowe 1992), possibly as part of a broadening of the Dahomey Gap (Moreau 1969:45). The orographic rain experienced in the east and on high ground would probably have compensated for the increased aridity during such savanna expansions (Hall 1977). Of course the savanna intrusions, in

addition to affecting the distributions of birds indirectly through its effect on the floral composition of the forest, possibly had a direct physical effect on individual bird species distributions, preventing their expansion further westwards. In addition to the Congolian species that curtail their ranges east of the Cross River, a number of species that occur throughout the Guineo-Congolian forest are absent in central and western Nigeria. Two such species occur widely throughout the Guineo-Congolian forests (*Bleda eximia* and *Sylvietta denti*), whereas three occur only in the eastern and western portions of the Disjunct District in the Congolian Province (*Zoothera* [*princei*] *princei*, *Apalis nigriceps*, and *Ploceus preussi*). Such species would again point to the unusual nature of the forests of western and central Nigeria as a determinant of distributions of bird species. If the Cross River and the Dahomey Gap have affected distributions of species absent in central and western Nigeria one would expect differentiation of the disjunct populations. This differentiation does occur in the cases of three superspecies pairs which have one representative each west of the Dahomey Gap and east of the Cross River (*Bathmocercus* [*cerviniventris*] *cerviniventris* and *rufus*, *Malimbus* [*racheliae*] *ballmanni* and *racheliae*, and *Picarthartes* [*gymnocephalus*] *gymnocephalus* and *oreas*), possibly indicating the role of the Dahomey Gap and Cross River as barriers affecting the distribution of birds in Nigeria. The action of the Cross as a physical barrier to some species is supported by the five superspecies pairs which meet at the Cross River (e.g. *Dendropicos* [*gabonensis*] *lugubris* and *gabonensis* and *Macrospheus* [*flavicans*] *kempi* and *flavicans*).

Although the Dahomey Gap is not identified as the primary forest division by the cluster analysis, it quite probably did represent a vicariance event at glacial peaks when it would have reached its maximum extent (e.g. Crowe & Crowe 1982). These effects are demonstrated by three superspecies pairs, with one member each occurring west and one east of the Dahomey Gap, namely *Ceratogymna* [*cylindricus*] *cylindricus* and *albotibialis*, *Criniger* [*olivaceus*] *olivaceus* and *ndussumensis*, and *Apalis* [*rufogularis*] *sharpei* and *rufogularis*. It has probably also acted as a dispersal barrier to a few species, although to a lesser degree than was formerly thought (e.g. Diamond & Hamilton 1980; Crowe & Crowe 1982), forming the eastern boundary of *Illadopsis rufescens* and the western boundary of *Dryoscopus* [*cubla*] *senegalensis*, *Muscicapa infuscata*, and *Malimbus* [*erythrogaster*] *erythrogaster*, none of which are

replaced by congeners on the other side of the Dahomey Gap. *Agelastes meleagrides*, which occurs only west of the Dahomey Gap, is replaced by *A. niger* east of Cross River. Recent data have disproved the Dahomey Gap as a dispersal barrier to at least one 'Congolian' species, *Nigrita luteifrons*, which has been confirmed to occur in both Ghana and Sierra Leone, and as a vicariance barrier to the species pair of *Muscicapa ussheri* (east of the Dahomey Gap) and *infuscata* (primarily west of the Dahomey Gap), with *ussheri* recently confirmed to occur in Nigeria (Dowsett & Forbes-Watson 1993). If this is the situation in arguably the best sampled taxon, i.e. birds, it is difficult to know to what extent sampling gaps may blur the currently 'clear' effect of the Dahomey Gap (and other 'barriers') noted for other taxa (e.g. Moreau 1969: frogs & mammals). In addition, almost as many bird species have subspecies which occur on both sides of the Dahomey Gap as those which have different subspecies either side of the Dahomey Gap, and numbers concerned are low (Moreau 1969:53). Some of the cases of subspecies straddling the Dahomey Gap were found in the Pycnonotidae (bulbuls), which are birds of the lowest forest stratum and may be expected to be heavily affected by a savanna gap (Moreau 1969). These examples are particularly surprising given that at the time of Moreau's study subspecies were often distinguished on size or melanin modifications, which characters have been shown to be capable of rapid development (see Moreau 1969:52), and consequently might be expected to be susceptible to small breaks in gene flow. As mentioned previously, the Dahomey Gap does contain forest patches (Keay 1959), although undoubtedly these forest patches have been reduced in size and quality in recent times through human activity (Robbins 1978). Moreau (1969) proposes that forest-savanna mosaic still flanks the true forest on either side of the Dahomey Gap, reducing the width of the savanna by half, providing, together with the various forest patches, an environment that a number of forest species not only seem able to cross, but also utilize (Robbins 1978; Burgess *et al.* in press; observations in this study). Of course, the flora and fauna of these forest patches in the Dahomey Gap are only depauparate versions of the true forest (Burgess *et al.* in press) and have even been considered by some to be mere relicts of the Guinea forest proper (but see Moreau 1969:42 for discussion). Moreau (1969) concludes that the Dahomey Gap has only on rare occasions acted as an insurmountable barrier to gene flow for sufficient a period as to allow divergence, even at subspecific level, which can happen readily (see example discussed above). Robbins (1978)

claims that the Dahomey Gap has had no influence whatsoever for forest mammals, but recent work by Burgess *et al.* (in press) shows this point of view to be a bit extreme . This study tends to agree with Moreau's (1969) views and finds that although, historically, the Dahomey Gap might well have prevented gene flow, particularly at one or two probable periods of heightened intensity (Moreau 1969:58), and has allowed some level of differentiation, most taxa have subsequently been able to re-establish gene flow. Very few cases are seen where gene flow inhibition has been maintained by the Dahomey Gap. One species is restricted to the west of the Dahomey Gap and two species are restricted to the east of the Dahomey Gap. However, in at least one instance such a pattern was shown to be due to sampling deficiency. The three superspecies pairs that meet at the Dahomey Gap could well be *maintained* by competition (*sensu* Moreau 1969:57; Diamond & Hamilton 1980).

Note that only two Congolian species reach the western extent of their range at the Dahomey Gap as compared to the roughly 19 species that do so at the Cross River. (Only one Congolian species reaches its western extent at the Niger River as discussed above).

5.3.4.1. Congolian Province

LOCATION AND AVIFAUNA

The Congolian Province consists of the Central, Disjunct, Gabon, Mt Cameroon and Inner Southern Congo Savanna Districts.

5.3.4.1.1. Central District

LOCATION AND AVIFAUNA

The Central District encompasses the upper reaches of the Congo River from Kivu westwards to where it drains Lake Tamba, and is predominated by wetter types of Guineo-Congolian lowland rain forest (W 1a), including swamp forest (W 8). The moist nature of the vegetation of this district, as compared with that of the other Congolian districts, is reflected in the habitat preferences of its four zone-restricted species. Two are restricted to humid forest (*Afropavo congensis* and *Apalis goslingi*) and two inhabit riparian forest (*Nectarinia corgensis* and *Brachycope anomala*).

5.3.4.1.2. Disjunct District

LOCATION AND AVIFAUNA

The Central District is bordered to the northeast and northwest by the Disjunct District, which consists of two disjunct portions roughly between 4°N and 1°S, the eastern portion being northeast of the Democratic Republic of Congo (including Ituri), the western portion encompassing southern Cameroon, Rio Muni, and northern Gabon. This district consists of wetter (W 1a) and drier (W 2) types of Guineo-Congolian lowland rainforest with mosaics of these types (W 3). Three of the four species that are restricted to the eastern portion are replaced by superspecific congeners at some point. *Platysteira* [*blissetti*] *jamesoni* is replaced in the western portion by *chalybea*. *Batis* [*minima*] *ituriensis* is replaced by *minima*, *occulta*, and *minulla*, which occur widely west of the Congo River. *Centropus* [*leucogaster*] *neumanni* is replaced by *anselli* on the southeastern side of the Congo River in the Cuvette Centrale, from where it extends into the western portion of the Disjunct District. *Malimbus flavipes* is not replaced by a congener. *Platysteira* [*blissetti*] *jamesoni*, *Batis* [*minima*] *ituriensis*, and *Malimbus flavipes* are typical of humid forest. *Centropus* [*leucogaster*] *neumanni* inhabits swampy bush and grass and the edge of dense secondary forest.

Six species are restricted to the western portion of the Disjunct District, three of which are replaced by congeners. *Platysteira* [*blissetti*] *chalybea* is replaced by *jamesoni* as discussed above. *Psalidoprocne* [*prisoptera*] *petiti* is replaced by *mangebetorrum*, which occurs just northeast of the eastern portion, but is probably an example of the east-west disjunction. *Bradypterus grandis* is replaced by *carpalis* on the eastern rim of the Congo basin, ranging into the Albertine Mountains. *Hirundo fuliginosa*, *Anthus pallidiventris*, and *Ploceus batesi* are not replaced by congeners. *Platysteira chalybea* is a species found in humid forest undergrowth, *Bradypterus grandis* is a bird of swamp and reedbeds, and *Ploceus batesi* is a little known bird of lowland forest. *Hirundo fuliginosa*, *Anthus pallidiventris*, and *Psalidoprocne petiti* are less stenotypic in their habitat use, either making use of man-made habitats, as in the case of the first two, or moist woodland, as in the case of the latter.

GENERAL POINTS

Although three species characterise the combined area of the Central and Disjunct Districts (*Prionops rufiventris*, *Muscicapa sethsmithi*, and *Malimbus cassini*), and a further three species are restricted to this combined area (*Melignomon zenkeri*, *Glaucidium sjostedti*, and *Spermophaga poliogenys*), there is much evidence to support the two districts as discrete avifaunal entities. This disjunction was first reported by Moreau (1966) and later observed by Crowe (1978), Diamond and Hamilton (1980), and Crowe and Crowe (1982), although the strength of its efficacy is contested by Louette (1984, but see discussion below). The occurrence of such a disjunction is supported in this study by the identification of a Disjunct District as separate from the intervening Central District, both of which have a number of species unique to them, as discussed above. A number of additional species display this disjunct distributional pattern, although they do not strictly qualify as zone-restricted. *Francolinus nahani*, *Zoothera oberlaenderi*, and *Phyllastrephus lorenzi* are affiliated with the eastern portion, and *Picathartes* [*gymnocephalus*] *oreas*, *Ploceus aureonucha*, and *Malimbus* [*racheliae*] *racheliae* are affiliated with the western portion. None of these are replaced in the opposite portion or in the intervening Central District by congeners.

Twenty-nine species occur in both the eastern and western portions of the Disjunct District, being absent from the intervening Central District, although none strictly meets the criteria of zone-restricted or characteristic species. All of these species are largely lowland species, although some range into the associated mountains of the Albertine Rift and Cameroon-Bameda Highlands. Montane species that occur on both the Albertine Rift and Cameroon-Bameda Mountains are not discussed here, as recent research (e.g. Roy *et al.* 1997) shows that speciation patterns in montane forest birds of the Afrotropics are complex, showing mixtures of leap-frog and 'shuttle' speciation, which can only be elucidated by detailed genetic work. Table 5.8 gives a full listing of lowland forest species showing an east-west disjunction

As with the other distributional patterns exhibited by the forest species investigated in this study, this disjunction is also somewhat affected by data errors, as pointed out by Louette (1984). However, only

Table 5.8. Lowland and montane forest species that show an east-west disjunction

LOWLAND FOREST SPECIES

Dendropicos poecilolaemus, *Phoeniculus castaneiceps*, *Apus batesi*, *Otus icterorhynchus*, *Bubo shelleyi*, *Smithornis sharpei*, *Campephaga petiti*, *Campephaga [lobata] oriolina*, *Laniarius [luehderi] luehderi*, *Platysteira concreta*, *Neocossyphus rufus*, *Zoothera cameronensis*, *Zoothera princei*, *Muscicapa epulata*, *Muscicapa tessmanni*, *Sheppardia cyornithopsis*, *Cercotricahs hartlaubi*, *Phyllastrephus xavieri*, *Criniger [barbartus] chloronotus*, *Criniger [olivaceus] ndussumensis*, *Apalis nigriceps*, *Bathmocercus [cerviniventris] rufus*, *Phyllanthus atripennis*, *Ploceus albinucha*, *Ploceus preussi*, *Ploceus dorsomaculatus*, *Ploceus insignis*, *Malimbus coronatus*, and *Estrilda* [*atricapilla*] *atricapilla*.

MONTANE FOREST SPECIES

Dendropicos elliotii and *Ploceus insignis*.

Species that show disjunct distributions, but which are not zone-restricted.

Apaloderma aequatoriale, *Cercotrichas hartlaubi*, *Baeopogon clamans*, and *Phyllastrephus xavieri*.

four of the species (*Dendropicos elliotii*, *Apaloderma aequatoriale*, *Calyptocichla serina*, and *Baeopogon clamans*) which this study identified as disjunct were shown to be continuous once additional data from Louette (1984, 1988a, 1988b, 1989, 1992) were added. Twenty species were confirmed by Louette (1984) to 'possibly show a distributional gap' (marked 'i', 'ni' or 's' in his Table 2), a further nine were not commented on in his (1984) study. Although Louette (1984, 1992) expressed reservations about the results obtained by the Crowe and Crowe (1982) study which identified a disjunction, he found only three of the species which they cited as showing disjunctions to have been misclassified, rather being continuous once additional data had been added. This study was cautious in identifying disjunctions, rejecting eight species that Louette identified in his 1984 study as possibly exhibiting a gap due to more recent data being added (Dowsett & Forbes-Watson 1993). Isolated records in the Central District for shy species were interpreted as probably indicating sampling deficiencies, such that these species were considered to probably *not* to show an east-west disjunction to be on the safe side (e.g. *Caprimulgus binotatus*).

A number of species showing an east-west disjunction in the Congolian forests also have populations in the Guinean forest, mostly only west of the Dahomey Gap (e.g. *Apalis nigriceps*, *Ploceus albinucha*, and *Ploceus preussi*). Others are replaced by congeners in the Guinean forest, again usually restricted to the

Upper Guinea (*Campephaga* [*lobata*] *oriolina* and *lobata*, *Criniger* [*olivaceus*] *ndussumensis* and *olivaceus*, and *Bathmocercus rufus* and *cerviniventris*). The most extreme case of congeneric replacement seen for this pattern is that of *Platysteira* [*blissetti*] *jamesoni* in the eastern portion of the Disjunct District, *chalybea* west of the Congo River and *blissetti* in the Guinean forest west of the Cross River. A less clear version of this pattern is exhibited by *Centropus* [*leucogaster*] *neumanni* in the eastern portion of the Disjunct District, *anselli* in the central basin and the western portion, being replaced by *leucogaster* in the vicinity of the Sanaga River, although there is some overlap along the western coast between the last two. These examples would seem to strengthen the idea of forest species having been restricted to refugia in the past in the Upper Guinea, Cameroon/Gabon area and the northeast of the Congo basin (Ituri), as proposed by Diamond and Hamilton (1980), Crowe and Crowe (1982), and Stuart *et al.* (1993), such that many current distributions may represent relaxations out of such refugia. If east-west disjunctions were found only within particular species' distributions, then one could argue that this pattern is *purely* due to extant differences in the nature of the forests of the east-west Disjunct District and those of the Central District, as suggested by Louette (1984). However, the occurrence of a number of superspecies groups which reflect this disjunction, despite inclusion of data from Louette (1984, 1988a, 1988b, 1989, 1992) for the central basin, would seem to support the existence of real gaps in distribution. Such refugia would have been separated by inhospitable vegetation which formed a complete barrier to gene flow, for sufficiently long to result in not only superspeciation, but possibly even full speciation of *Bradypterus grandis* and *carpalis* (although admittedly both species probably suffer from insufficient sampling, and it is difficult to ascertain whether these two species are indeed each other's closest relatives). As discussed above, a concerted effort was made to check that these distributional gaps are, to the best of current knowledge available to this study, real and not just due to data omissions. In addition, identification of species as disjunct was conservative (i.e. when in doubt, leave out).

That gene flow is currently maintained between the disjunct populations of a number of species, seems likely as few subspecific disjunct replacements were cited by Crowe and Crowe (1982), who included 'well marked subspecies' as entities of their study. Louette (1984) found only subspecific differentiation

between the eastern and western populations in 5 of the 30 species he identified as possibly having a distributional gap. Just how gene flow between populations is currently maintained is not clear. Various bridges to the north and south have been proposed, primarily based on the distributions of species, which although mainly confined to the eastern and western portions of the Congolian forest, show such 'bridges'. A northern 'bridge' joining the two portions of the Disjunct District is seen in *Guttera plumifera*, *Agelastes niger*, and *Psalidoprocne chalybea*. The 'bridge' possibly seen in *Guttera plumifera* is the most northerly situated, coinciding with the Ubangi-Uelle Savanna Province (named after Chapin 1932). The Ubangi-Uelle Savanna Province follows the slight escarpment proposed by Moreau (1966) to have been a link for montane forest birds in the past. The existence of such a link is contested by Diamond and Hamilton (1980). *Lanius mackinnoni*, a woodland and forest edge species, shows a possible southern bridge. However, when looking for a 'bridge', one is really looking for something that could join true, stenotypic forest species of the dark, moist undergrowth, as is utilized by three true forest interior species with disjunct distributions (e.g. *Criniger chloronotus*). It is possible that exchange takes place through the Central District, with the numbers of individuals involved being either too small, spending too little time in the intervening area, or being too cryptic to have been recorded (Louette 1984).

The Congo River itself does not seem to have played a large role as a vicariance or dispersal barrier, with few species being confined by it. *Agelastes [meleagrides] niger, Bubo [poensis] poensis*, and *Camaroptera chloronata* occur predominantly north of the river, only dispersing to a limited degree around the river mouth. None of these are replaced by congeners on the southern side of the river. Interestingly enough, the lower reaches of the Congo River near its mouth seem to prevent eastward expansion of a few forest species predominantly confined to the Guinean forest (e.g. *Gymnobucco peli*). The Congo River has, however, possibly acted to slow or prevent complete colonisation of the Central District, or Cuvette Centrale, by species expanding out of the Mt Cameroon-Gabon and Ituri refugia, as suggested by Jenkins (1992) (e.g. *Stiphrornis erythrothorax*, *Sheppardia cyornithopsis*, and *Cossypha cyanocampter*). A number of species occurring widely throughout both the Guinean and Congolian Provinces do not occur along the banks of the main part of the Congo River (e.g. *Tockus camurus*,

Merops muelleri, *Smithornis rufolateralis*, and *Myioparus griseigularis*). This is possibly due to differences in the vegetation composition and structure.

5.3.4.1.3. Gabon District

LOCATION AND AVIFAUNA

This district, as its name indicates, is coincident with the country of Gabon. It has one zone-restricted species, *Ploceus subpersonatus*.

GENERAL POINTS

The nonpasserine cluster analysis identifies the Gabon District as part of the western portion of the Disjunct District. This is partially due to the lack of nonpasserines restricted to the Gabon area, but also due to a number of species that occur along the 'armpit' of West Africa (*sensu* Kingdon 1989), that is from the Congo River north along the coast to the Guinea forests (e.g. *Centropus leucogaster*). The passerines, however, identify the Gabon District as a distinct entity, partly due to the presence of the zone-restricted *Ploceus subpersonatus*, mentioned above.

5.3.4.1.4. Mt Cameroon District

LOCATION AND AVIFAUNA

The Mt Cameroon District consists primarily of Mt Cameroon and Mt Kupe, and their immediate surrounds. This district is strongly defined at a BC = 0.20 with five zone-restricted species, four of which are confined to Mt Cameroon (*Francolinus camerunensis*, *Psalidoprocne fuliginosa*, *Speirops melanocephalus*, and *Bradypterus lopezi*). *Telophorus kupeensis* is also found on Mt Kupe. All are birds of montane forest.

GENERAL POINTS

Note that this district does not include the Bameda Highlands of southwestern Cameroon and the Obudu Plateau of southeastern Nigeria, which fall under the Southwestern Province of the Northern Savanna Subregion. The high tallies of zone-restricted species that might be expected to occur in the Mt

Cameroon District are listed in Table 5.9. This list includes the 18 species restricted to the greater Cameroon-Bameda Highland system that spans the Mt Cameroon District of Guineo-Congolian Subregion and the Southwestern Province of the Northern Savanna Subregion. The majority of these species are forest specialists (e.g. *Columba sjostedti*, *Phyllastrephus poensis*, and *Kupeornis gilberti*. Five use either forest edge (*Ploceus bannermani*), wooded ravines, grassland (*Anthus camaroonensis*), heath (*Cisticola discolor*) , or some combination thereof (*Urolais epichlora* and *Neocharis shelleyi*).

Table 5.9. Species restricted to the greater Cameroon-Bameda Highland system, which spans the Mt Cameroon District of Guineo-Congolian Subregion and the Southwestern Province of the Northern Savanna Subregion. ^{B} = species, which although primarily restricted to the Southwestern Province of the Northern Savanna Subregion, also range across the Mt Cameroon District of the Guineo-Congolian Subregion. ^{C} = species, which although primarily restricted to the Mt Cameroon District of the Guineo-Congolian Subregion, also range into the Southwestern Province of the Northern Savanna Subregion.

Tauraco bannermani, *Columba sjostedti* ^{B}, *Laniarius atroflavus* ^{B}, *Malaconotus gladiator* ^{B}, *Platysteira laticincta*, *Zoothera crossleyi* ^{C}, *Cossypha isabellae* ^{B}, *Coccycolius iris*, *Psalidoprocne fuliginosa* ^{C}, *Andropadus montanus* ^{B}, *Phyllastrephus poensis* ^{B}, *Phyllastrephus poliocephalus* ^{B}, *Cisticola discolor* ^{C}, *Urolais epichlora*, *Apalis Bamedae* ^{B}, *Poliolais lopezi* ^{C}, *Phylloscopus herberti* ^{C}, *Kupeornis gilberti* ^{C}, *Nectarinia oritis* ^{B}, *Nectarinia ursulae* ^{C}, *Anthus camaroonensis* ^{B}, *Ploceus bannermani* ^{B}, *Malimbus ibadanensis*, and *Nesocharis shelley* ^{B}.

The failure of the Cameroon-Bameda Highland system to be recognised as a distinct avifaunal unit completely contained within the Guineo-Congolian Subregion (as suggested by Chapin 1932) is due to the failure of the scale of this study to be able to distinguish between montane and lowland avifaunas contained in the same grid cell. The avifauna of the portion of the Bameda Highlands that falls into grid cells classified by the cluster analysis as the Southwestern Province of the Northern Savanna Subregion are numerically dominated by the large lowland woodland avifauna that also occurs in these grid cells (the district has a total of 451 species, Table 5.3).

5.3.4.1.5. Inner Southern Congo Savanna District

See discussion of forest-savanna transition on the northern border of the *Brachystegia* belt avifauna under the Southern Savanna Subregion.

5.3.4.2. Guinean Province

LOCATION AND AVIFAUNA

The Guinean Province is identified by the cluster analysis as the forest area west of the Cross River. It has four characteristic species, all of which are absent from the Dahomey Gap. The six zone-restricted species show varying degrees of tolerance to the Dahomey Gap - *Melignomon eisentrauti* and *Muscicapa ussheri* are completely absent therefrom, whereas *Phyllastrephus baumanni* occurs marginally therein, and *Dendropicos pyrrhogaster*, *Prionops caniceps*, and *Nectarinia adelberti* occur through the Dahomey Gap.

GENERAL POINTS

Various barriers and refugia are postulated to have affected the patterns of distribution of many taxa in the Upper Guinea. Barriers suggested include the Sassandra (or Cavally) River (e.g. Moreau 1969: forest vertebrates; Happold 1996: mammals), the Baoule-V savanna intrusion centred on the Bandama River in central Cote d'Ivoire (e.g. Kemp & Crowe 1986: galliforms and hornbills), and the savanna break in the forest of the Dahomey Gap (e.g. Moreau 1969: forest vertebrates; Kemp & Crowe 1986; Short & Horne 1986: Piciformes). The Baoule-V, which currently reaches to within 150 km of the coast, possibly represents a complete break in earlier times (Jenkins 1992). Probable causes of the Baoule-V include the rain shadow effect, resultant from a change in the orientation of the West African coastline (e.g. Vooren 1992). Proposed refugia include the western or Liberian refugium west of the Sassandra River (e.g. Happold 1996: forest mammals, Crowe & Crowe 1982: terrestrial Afrotropical birds) or Sierra Leone (Diamond & Hamilton 1980: forest passerines), and the eastern Ivory Coast/western Ghana (Ghanaian) refugium (Diamond & Hamilton 1980; Happold 1996). Vooren (1992) suggests that the latter refugium possibly consisted of two noda at Cape Three Points and Cape Palmas specifically.

Two Afrotropical bird species are restricted to the forests west of the Sassandra River, namely *Melaenornis annomarulae* and *Phyllastrephus leucolepsis*. Another (*Laniarius* [*ferrugineus*] *turatii*) is even more restricted, only occurring west of Kenema (Sierra Leone), supporting the idea of a refugium

(centre of endemism) in the Sierra Leone-Liberia area. However, the role of the Sassandra River itself as a barrier (rather than the patterns being due to the existence of a western refugium) is difficult to investigate. Only a single species (*Merops malimbicus*) has its western boundary directly east of the Sassandra River. This could well be a sampling artefact, as *Gymnobucco* [*peli*] *peli*, which was thought to exhibit the same pattern, has been shown by more recent data (Dowsett & Forbes-Watson 1993) to occur as far west as Sierra Leone. This was also the case for 11 species thought to only occur east of Kenema until the Dowsett & Forbes-Watson (1993) data were added. Five species appear to have their western limit somewhere between the Sassandra River and Kenema, with a further seven appearing to curtail their ranges east of Kenema. It is quite likely that this graded pattern is a sampling artefact given the number of species whose distributional pattern had to be reclassified once Dowsett and Forbes-Watson (1993) data were added. It is likely that further changes would be called for if all the field data collected since 1993 were to be added. For instance, work by the Centre for Tropical Biodiversity, Denmark, added a number of records for species in Ghana which were previously thought to show a discontinuity between the Sassandra River and the Dahomey Gap or the Volta River.

It is possible that the Baoule-V has acted as a dispersal barrier, with two species reaching their western boundary at this point, namely *Prinia* [*leucopogon*] *leontica* and *Pyrenestes* [*ostrinus*] *sanguineus*. Again, a discontinuity between the Baoule-V and the Dahomey Gap exhibited by *Glaucidium* [*castaneum*] *castaneum* is brought into question with the addition of new records for *Indicator exilis*, which was previously thought to also exhibit this pattern. It is difficult to know whether similar additional data for other biota which have been identified as displaying these patterns of barriers and refugia will change the situation for them too.

5.3.4.2.1. Upper Guinea District

LOCATION AND AVIFAUNA

The Upper Guinea District, west of the Dahomey Gap, includes montane vegetation (W 19a) found on the isolated mountain peaks of Bintumani (Loma Mountains), Sankan Biriwa (Tingi Mountains) Nimba,

Macenta, Niete, and Uni. This district has three characteristic species and 10 zone-restricted species. Only one of the zone-restricted species, namely *Prinia leontica*, uses the mountain forest habitat present on the aforementioned mountain peaks.

5.3.4.2.2. Lower Guinea District

LOCATION AND AVIFAUNA

The Lower Guinea District represents a transitional avifauna between the Dahomey Gap and the Cross River, and is therefore defined by default. Details of avifaunal patterns within this district are discussed above under the avifaunal complexities of the Nigerian forest.

5.3.4.3. Ubangi-Uelle Savanna Province

LOCATION AND AVIFAUNA

The Ubangi-Uelle Savanna Province stretches along the slight escarpment on the northern rim of the Congo basin from 23°E to 12°E on the border of the Democratic Republic of Congo and the Central African Republic. It has no characteristic or zone-restricted species, being a default zone that represents the transitional area between the Guineo-Congolian forest avifauna and Northern Savanna savanna-woodland avifauna.

GENERAL POINTS

The Ubangi-Uelle Savanna Province is named after Chapin (1932) who commented on the abrupt nature of this transition (Chapin 1932:85). It is characterized by high species replacement that takes place along a narrow front, as is discussed above under the northern forest-savanna transition in the general points of the Guineo-Congolian Subregion.

5.3.4.4. Albertine Rift Province

LOCATION AND AVIFAUNA

The Albertine Rift Province is named after Jenkins (1992: defined as eastern Zaire, Rwanda, Burundi, and Uganda) and Stuart *et al.* (1993) to describe the mountains that run from Mt Bleus (northwest of

Lake Albert) along the Albertine Rift to the Marungu mountains (southeastern Democratic Republic of Congo). This vegetationally diverse district forms a transition between forest (W 2, 11a) and various woodlands and savannas (W 29a, 35b, 42, 45), lowland and montane elements (W 19a). It also encompasses the Lake Victoria transition mosaic (W XII). Of the 57 species restricted to this district, 40 are restricted to the mountains west of Lake Tanganyika (marked ^{A} in Appendix 5.1). A further 13 extend from these mountains to those of western Uganda and Kenya (Ruwenzoris, Aberdares, Mt Kadam, Mt Elgon, and Mt Kenya) and southeastern Sudan (Mt Kinyeti) (these species are unmarked in Appendix 5.1). Most of these 13 species are forest dwelling (e.g. *Sheppardia aequatorialis*, *Sylvietta leucophrys*, and *Phylloscopus budogoensis*), although a few occur in nonforest montane habitats such as heath and bracken (*Telophorus dohertyi* and *Cisticola chubbi*), grassland (*Anthus latistriatus*), papyrus beds, elephant grass, and woodland thicket (*Eminia lepida*). Three of the species restricted to this district are lowland species, two of which (*Ploceus victoriae* and *Serinus koliensis*) are restricted to the papyrus swamps of Lake Victoria (marked ^{LV} in Appendix 5.1) and a third (*Lybius rubrifacies*) which inhabits *Combretum* bush and the gallery forest west of Lake Victoria.

5.3.5. Southwestern Subregion

LOCATION AND AVIFAUNA

Stretching from the Drakensberg mountains in the east (around 29°E) to 12°N on the western coast of Africa down to the southern coast of Africa, the Southwestern Subregion encompasses five avifaunal zones, spanning a range of vegetation types from the Namib desert (W 74) through Karoo and Fynbos shrubland (W 50, 51, 52, 53) to mopane and Kalahari woodland (W 28, 44) and Highveld grassland (W 58). Most of the 12 species characteristic of this subregion use the full range of these habitats (e.g. *Colius colius*, *Batis pririt*, *Serinus falviventris*, and *Emberiza impetuani*), as do some of the 45 species which are restricted to this subregion, but which are not confined to any one of its avifaunal zones (e.g. *Bradornis infuscatus* and *Malcorus pectoralis*). Other species restricted to this subregion use various combinations of these habitats, such as the desert scrub of the Namib and Karoo (e.g. *Cercomela*

schlegelii), Karoo and grasslands (e.g. *Spreo bicolor*), Karoo and Fynbos (e.g. *Parus afer* and *Cisticola subruficapillus*), Fynbos and Highveld grassland (e.g. *Francolinus africanus*), Karoo, mountain Fynbos and thornveld (e.g. *Stenostira scita*), and Fynbos, Highveld and thornveld (e.g. *Mirafra apiata*). Quite a few of these zone-restricted species are generalists that make use of man-made habitats such as exotic plantations, urban gardens and farmlands (e.g. *Telophorus zeylonus*, *Sigelus silens*, *Zosterops pallidus*, and *Passer motitensis*).

The Highveld, Karoo, and Fynbos Districts are all closely related with the Highveld and Karoo Districts clustering at BC = 0.32, and the Fynbos District joining the aforementioned grouping at BC = 0.39. They are perhaps better considered as a Fynbos-Karoo-Highveld Province, characterised by *Cercotrichas coryphaeus* and *Galerida magnirostris*.

5.3.5.1. Highveld-Karoo-Fynbos Province

Location and avifauna

The Highveld, Karoo, and Fynbos Districts of the Highveld-Karoo-Fynbos Province share a similar avifauna (BC = 0.39). The province is supported by the characteristic species of *Cercotrichas coryphaeus* and *Galerida magnirostris*. However, each district forms a discrete entity with its own zone-restricted and characteristic species (Appendix 5.1).

General points

This arrangement retrieves the avifaunal zonation suggested by Winterbottom (1978) for southern African birds almost exactly. However, the cluster analysis distinguishes the Namib avifauna as distinct from the Highveld-Karoo-Fynbos grouping, whereas Winterbottom (1978) suggests that the Namib is an impoverished version of the Karoo. Within the Highveld-Karoo-Fynbos Districts, the closer relation of the Highveld and Karoo is due to the eurotypy of a number of Karoo birds that extend their ranges into the Highveld (Clancey 1986), as seen in *Grus paradisea* and *Cercomela sinuata*.

5.3.5.1.1. Highveld District

LOCATION AND AVIFAUNA

This district matches the Highveld grassland (W 58) almost perfectly and its four zone-restricted species are all montane grassland specialists, namely *Eupodotis caerulescens*, *Geronticus calvus*, *Chaetops aurantius*, and *Serinus symonsi*. *Eupodotis caerulescens* shows marginal intrusion along the Highveld grassland patches into the Karoo district.

5.3.5.1.2. Karoo District

LOCATION AND AVIFAUNA

Although vegetation types found in this district range from the predominant dwarf and succulent Karoo shrubland (W 53, 52), to bushy Karoo-Namib (W 51) and grassy montane (W 57a), with a transition from grassy montane Karoo shrubland to Highveld (W 57b), zone-restricted and characteristic species are mainly associated with the drier types of desert or semi-desert vegetation (*Eupodotis vigorsii*, *Neotis ludwigi*, *Spizocorys sclateri*, and *Certhilauda burra*) or dry river courses (*Euryptila subcinnamomea* and *Eremomela gregalis*).

5.3.5.1.3. Fynbos District

LOCATION AND AVIFAUNA

This district comprises the majority of White's Fynbos (Cape shrubland) regional centre of endemism (W 50). The avifauna of this district is characterised by Fynbos specialists, of both lowland and montane type (*Bradypterus victorini*, *Promerops cafer*, *Nectarinia violacea*, and *Serinus leucopterus*), with one characteristic species of montane grassland (*Turnix hottentota*) and one zone-restricted species of rocky areas (*Chaetops frenatus*). Two typically Fynbos species have enlarged their ranges to utilise man-made habitats such as wheatfields (*Francolinus capensis*) and exotic plantations and urban gardens (*Pycnonotus capensis*) so that they are not considered as restricted to this district.

GENERAL POINTS

A number of forest and forest-edge species range from the Fynbos District along the coast of the

Tongaland-Pondoland District of the Southern Savanna Subregion and then inland along the mountains into southern Zimbabwe and Mozambique (*Campethera notata*, *Tauraco corythaix*, *Tchagra tchagra*, *Batis capensis*, *Bradypterus sylvaticus*, and *Serinus scotops*), some extending west, probably along the Limpopo River, into the eastern portion of the Kalahari Province (*Laniarius ferrugineus*, *Nectarinia chalybea*, *N. afra*, and *Estrilda melanotis*). A similar distributional pattern is seen in species associated with coastal and montane Fynbos and grassland (*Francolinus africanus*, *Sphenoaecus afer*, *Macronyx capensis*, and *Ploceus capensis*).

5.3.5.2. Kalahari Province

LOCATION AND AVIFAUNA

This province is so named due the predominance of Kalahari *Acacia* wooded grassland and deciduous bushland (W 44). It also contains patches of *Colophospermum mopane* woodland and scrubland (W 28) to the northeast and northwest, with transitions between these and to Karoo-Namib shrubland and Zambezian undifferentiated woodland (W 36, 56, 35a). The majority of characteristic species occur in the 'thornveld', that is the arid *Acacia* savanna parkland or woodland typical of South Africa north of the Orange River, central Namibia and Botswana (e.g. Sinclair *et al.* 1993) (*Cercotrichas paena*, *Lamprotornis australis*, *Calamonastes fasciolatus*, and *Turdoides bicolor*), as does the zone-restricted *Certhilauda chuana*, and a number of species, which although not restricted to the Kalahari district per se, have their distributions centred around this region (*Eurocephalus anguitimens*, *Bradornis mariquensis*, *Mirafra passerina*, *Spizocorys conirostris*, and *Uraeginthus granatina*). Four of the eight species restricted to this district are found in the rocky, hilly and mountainous regions that run in a narrow band from southwestern Angola to northwestern Namibia (*Francolinus hartlaubi*, *Tockus monteiri*, *Namibornis herero*, and *Achaetopus pycnopygius*).

GENERAL POINTS

Winterbottom (1978) identifies the Kalahari Province as the 'South West Arid District' which does not include the Karoo and Namib (supported by Poynton 1995). If Winterbottom is correct in stating that the Karoo avifauna is distinct from that of the 'South West Arid District', it may well explain why botanists

have recently suggested that the arid corridor has played little to no role in determining the origins of the Karoo flora (e.g. Hilton-Taylor 1987). Van Zinderen Bakker (1969), the original proponent of the existence of an 'arid corridor' proposes that the southwestern avifauna inhabits the Kalahari and Namib, but does not extend the area south to include the Karoo. Perhaps this is what Thulin and Johansson's study (1996; see also Thulin 1994) of the genus *Wellstedia* best supports.

5.3.5.3. Namib Province

LOCATION AND AVIFAUNA

The Namib Province consists mainly of the Namib Desert (W 74) with some bushy Karoo-Namib shrubland (W 51) in the east. Both species restricted to this district, *Certhilauda erythrochlamys* and *C. barlowi*, use the gravel plains and scrub desert of coastal Namibia, as do the near-endemics *Eupodotis rueppellii* and *Ammomanes grayi*.

GENERAL POINTS

A few larks extend from the Karoo District into the Namib Province, resulting in these two zones being defined as closely related by the passerines. The nonpasserines, which define the Karoo more tightly, identify the Namib as most closely related to the large Kalahari Province. These two patterns combine to result in the Namib being defined as peripheral to all other districts in the Southwestern Subregion.

ARID CORRIDOR

The basal position of the Southwestern Subregion in the dendogram emphasises the unusual nature of its avifauna, as does its six unique genera. Five of these genera are represented by a single species each, namely *Lanioturdus torquatus*, *Namibornis herero*, *Euryptila subcinnamomea*, *Stenostira scita*, and *Philetairus socius*, while one has undergone radiation, namely *Certhilauda* (Certhilauda [*curvirostris*] *curvirostris* and *chuana*, *C.* [*albescens*] *erythrochlamys* and *albescens*, *C. burra*, and *C. barlowi*). The uniqueness of this avifauna is further emphasised by Clancey's (1986) observation that 70% of birds endemic to southern Africa are restricted to the 'Southwestern Arid Zone'. However, this basal position is somewhat surprising in light of the affiliation noted for a number of taxa between the arid and semi-

arid parts of the Southwestern and Northeastern Subregions (e.g. Winterbottom 1967 & Clancey 1986: birds; de Winter 1971: flora; Hilton-Taylor 1987: phytogeography of the Karoo; Poynton 1995: genus *Bufo*, Thulin 1994: Somali flora; Thulin & Johansson 1996: genus *Wellstedia*). Currently, these areas are linked by a 'drought corridor' of land that receives less than 10mm of rainfall per month for at least three consecutive months (Balinsky 1962). Vegetation in this 'drought corridor' varies from dry forest to desert (Balinsky 1962). It is proposed that, in past drier episodes, the aridification of vegetation in this drought corridor would have allowed exchange of, and resulted in affinities of, both flora and fauna of the arid and semi-arid regions of Northeast (centred on Somalia) and Southwest (centred on Namibia) Africa (e.g. Balinsky 1962). Connection between the true desert elements of the Namib and the 'Sahara-Sindic' region must be very old (van Zinderen Bakker 1969), possibly occurring during the Tertiary (Thulin 1994; see Hilton-Taylor 1987 for review), with the semi-arid elements of the Kalahari (and Karoo) and East Africa being more recent (van Zinderen Bakker 1969). However, the timing, duration, and frequency of the opening of the arid corridor are not certain (see Hilton-Taylor 1987). Winterbottom (1967) suggests that there must have been a number of connections as relations are seen at all levels, from disjunct populations to full species. Unfortunately, Winterbottom (1967) does not give a full list of species he deems to reflect these patterns. Species considered by this study to exhibit arid corridor distributions are listed in Table 5.10 (those mentioned by Winterbottom, 1967, are marked ^{W}).

Table 5.10 illustrates the strong avifaunal links of the arid regions of northeastern and southwestern Africa, with disjunctions at population level shown by three species, at subspecies level by two species, at superspecies level by five species, and at full specific level by five species. The arid corridor has clearly had an effect on the avifaunal *composition* of both regions. It is difficult to tell what role this event has had in determining the *origins* of the avifauna of these regions and whether the northeast or southwest would have acted as the source, although Clancey (1986) suggests a strong northeast to southwest relation.

Table 5.10. Species which show affinities between the Northeastern and Southwestern Subregions. Square brackets indicate superspecies name. W indicates those mentioned by Winterbottom (1967).

SPECIES WITH DISJUNCT POPULATIONS:
Ardeotis kori W ,*Polihierax semitorquatus* W, and *Ploceus rubiginosus.*

SPECIES WITH DISJUNCT POPULATIONS THAT ARE SUBSPECIFICALLY DIFFERENTIATED (NORTHEAST: SOUTHWEST):
Francolinus levaillantoides gutturalis : levaillantoides W
Phoeniculus damarensis grant : damarensis

SUPERSPECIES PAIRS EACH WITH ONE MEMBER IN THE NORTHEAST AND ONE IN THE SOUTHWEST:
Tockus [flavirostris] flavirostris : leucomelas
Apus [pallidus] berliozi : bradfieldi
Eupodotis [ruficrista] gindiana : ruficrista
Melierax [canorus] poliopterus : canorus
Eurocephalus [anguitimens] rueppelli : anguitimens W
Uraeginthus [granatina] ianthinogaster : granatina W

SPECIES WHICH ARE SPECIFICALLY DISTINCT ALTHOUGH OBVIOUSLY CLOSELY RELATED (SENSU WINTERBOTTOM 1967:77) WITH ONE IN THE NORTHEAST AND ONE IN THE SOUTHWEST:
Pterocles decoratus : bicinctus
Bradornis microrhynchus : infuscatus W
Oenanthe monticola : phillipsi
Spreo fischeri : bicolor
Serinus dorsostriatus : flaviventris

5.3.6. Northern Arid Subregion

LOCATION AND AVIFAUNA

The Northern Arid Subregion consists of the Northern Arid and Horn of Africa Provinces. Their similarity is due both to a number of shared species as well as to the depauparate nature of their avifauna. In particular, a number of 'arid corridor species' extend into both these zones, as is the case for certain plants (Thulin 1994). However, there are no Afrotropical endemic species that are restricted to or characteristic of the Northern Arid Province. This is somewhat to be expected due to the situation of this province at the very north of the study region, but is also attributable to its extremely arid character.

5.3.6.1. Northern Arid Province

LOCATION AND AVIFAUNA

Few terrestrial Afrotropical endemic species extend their range as far as the absolute desert of the Sahara (W 67) that constitutes this province, such that this province is defined by default.

5.3.6.2. Horn of Africa Province

LOCATION AND AVIFAUNA

The Horn of Africa Province, which primarily covers the portion of the Haud (Ogaden) Plateau that does not fall into the Somali-Masai District of the Northeastern Subregion, is well characterized by the one characteristic species, *Sylvietta philippae*. *Eupodotis humilis* and *Oenanthe phillipsi* are nearly restricted to this district, extending only marginally into the Somali-Masai District of the Northeastern Subregion. The aforementioned three species all inhabit the *Acacia* savanna. Semi-desert grassland and shrubland (W 54b) covers the Nugal depression and Obbia coastline, providing habitat for three of the six zone-restricted species, namely *Mirafra somalica*, *Alaemon hamertoni*, and *Spizocorys obbiensis*. This arid habitat extends down along the coast of Kenya, as demonstrated by *Apus berliozi*. Northeast of the Nugal depression, the Warsengelia Highlands support Juniper forest, which has a zone-restricted species, *Carduelis johannis*. This highland also provides habitat for another two zone-restricted species - rocky ravines and caves for *Columba oliviae*, and open savanna for *Buteo archeri*. Three species, chiefly found in short grass plains, are restricted to this district, baring a disjunct population in the arid north of Kenya (*Calandrella somalica*, *Pseudalaemon fremantlii*, and *Passer castanopterus*). Some of the possible vicariance events relevant to this zone are discussed above under the Northeastern Subregion.

5.4. Discussion

Avifaunal patterns

The major subregional divisions suggested by the cluster analysis are supported by results from a divisive classification technique (Williams *et al.* in press), indicating that results presented in this study are robust to different hierarchical algorithm techniques. In addition, high scores of species replacement coincide with most of the subregional boundaries identified in this study. Thus, subregions represent discrete biogeographical entities, separated by transition zones where high turnover of species (i.e. replacement of one avifauna by another) takes place.

The subregions broadly coincide with major phytochoria and their regional centres of endemism as defined by White (1983). Although this is partly intuitive, and has been noted in other biogeographical studies of Afrotropical birds (Chapin 1932; Crowe & Crowe 1982) and African mammals (Turpie & Crowe 1994), some caution in interpretation is necessitated by the fact that many range maps for birds are interpolated from point data along expanses of similar vegetation. Although this study made a concerted effort to be conservative in interpolation of point data, these effects due to range interpolation cannot be completely ruled out.

The primary divisions of the dendrogram are between the more arid subregions (Northern Arid and Southwestern) and more mesic subregions (Northeastern, Southern Savanna and Northern Savanna and Guineo-Congolian) (Fig. 5.2b). The Northern Arid Subregion is particularly different, showing approximately only a 12.4 % similarity (BC = 0.88) to the other subregions. The division between the more arid and mesic subregion is in part due to the low species richness values of the more arid subregions and large amount of species 'drop outs' (i.e. species reaching the end of their ranges without being replaced by other species). A number of species occur widely in the Afrotropics except for these arid subregions (e.g. *Ispidina picta*, *Halcyon senegalensis*, *Oxylophus levaillantii*, *Myioparus plumbeus*, and *Ploceus cucullatus*). These trends of decreasing species richness result in comparatively low species richness values of 44 and 127 for the Northern Arid and Southwestern Subregions respectively, compared with that of 319 and 409 species in the Guineo-Congolian and Southern Savanna Subregions respectively. Low species richness acts to decrease the effective species pool from which relationships between grid cells can be formed. This affects the strength of relationships between species-poor and species-rich subregions, as well as zones within species-poor subregions. However, despite these factors, the arid subregions do represent discrete avifaunas with unique elements, as attested to by the existence of species restricted to and characteristic of these subregions. In addition, high levels of species replacement between the Southwestern and Southern Savanna Subregion, and between the Horn of Africa Province of the Northern Arid Subregion and the Northeastern Subregion emphasise that the avifauna of the Southern Savanna Subregion is *replaced* to the southwest by species unique to the Southwestern Subregion and to

northeast by species unique to the Horn of Africa Province of the Northern Arid Subregion.

As noted by Moreau (1935), Crowe and Crowe (1982), and Williams *et al.* (in press.), Afrotropical birds show a division between the avifaunas of the savannas (Northern Savanna, Southern Savanna, and Northeastern Subregions) and that of the forest (Guineo-Congolian Subregion). However, the cluster analysis suggests that the difference is not as large as is often cited (e.g. Moreau 1935) - the Guineo-Congolian Subregion shows only a 2.90 % difference from the savanna grouping (Fig. 5.2b). The relations between the savanna subregions are strengthened by the large number of species that occur in all nonforest and nondesert habitats (e.g. *Struthio camelus*), ranging through the Northeastern, Northern Savanna and Southern Savanna Subregions.

Pomeroy and Ssekabiira (1990) suggested that passerines divide the Afrotropics more finely than nonpasserines, but this trend was not clearly evident in this study, which found that the passerines and nonpasserines define approximately the same number of zones (compare Figs. 5.3 & 5.4). However, the passerines do define one extra zone in the Guineo-Congolian Subregion that the nonpasserines do not define, namely the Gabon District. On the other hand, nonpasserines define the southern forest-savanna transition as consisting of two clear parts (*viz.* the Inner Southern Congo Savanna District in the Guineo-Congolian Subregion and the Outer Southern Congo Savanna Province in the Southern Savanna Subregion), which is congruent with the studies of Chapin (1932) and Lynes (1938). The passerines only define one large southern forest-savanna transition zone within the Guineo-Congolian Subregion and a very small, fragmented forest-savanna transition zone in the Southern Savanna Subregion. The ordering of districts within subregions, and the relation of subregions to each other, differs between passerines and nonpasserines, but these differences are probably not significant. Most districts and subregions are defined at similar BC values by passerines and nonpasserines, although the passerines do define the Southwestern and Northeastern Subregions more strongly. This is probably purely due to the fact that, in relatively species-poor areas, fairly small fluctuations in the numbers of species available from which to infer similarity relations will affect the strength with which districts, provinces, and subregions can be

defined. As there are more than twice as many passerines as nonpasserines, it is perhaps not surprising that the passerines define some subregions more strongly than do nonpasserines. Note that, when the database containing all endemics species is divided into the smaller subsets of the passerines and nonpasserines, the already species-poor Northern Arid Subregion lands up with too few species from which meaningful patterns and relationships between grid cells can be derived. The results of this study indicate that similar patterns of distribution for nonpasserines and passerines is in keeping with results obtained by Crowe and Crowe (1982). These results are somewhat in contradiction to work by Pomeroy and Ssekabiira (1990) that suggests that distributional patterns of passerines differ to those of nonpasserines due to their more recent speciation history (e.g. Moreau 1966). Recent molecular studies suggest that the passerines may in fact not be the product of a few recent and rapid radiations, and may be as old as some of the nonpasserine species (J. Fjeldså pers. comm.) Analysis of distributional patterns in this study would seem to suggest that differences in speciation patterns between passerines and nonpasserines are not large, or that both groups have had sufficient time to redistribute after speciation events to reflect patterns of current environmental carrying capacity and, possibly, dispersal barriers.

Methodological draw backs

One disadvantage of the approach adopted in this study to define biogeographical patterns, is its failure to distinguish between distinct avifaunas that may occur at different altitudes within the same grid cells. For instance, the cluster algorithm cannot distinguish the avifauna of the Eastern Arc mountains from the avifauna of the surrounding Somali-Masai lowland steppe, which avifaunas co-occur in a number of grid cells. Whether this area of grid cells is classified as containing an Eastern Arc montane or Somali-Masai lowland avifauna largely depends on which species the analysis is based. Passerines emphasise the Eastern Arc montane elements while nonpasserines emphasise the Somali-Masai lowland elements. This problem is common to any 'flat' GIS (Geographical Information System) approach that cannot discriminate between altitudinal zones (e.g. Prendini 1995). More examples of this sort of problem are discussed in relevant sections below.

Where has speciation taken place and what has driven speciation?

Among the biogeographical literature in ornithology, authors who postulate specific mechanisms of genetic differentiation leading to speciation are few. Hall (1972) suggests that speciation among birds in Africa takes place through a cycle. First, there is the *emergence* of a new species through the acquisition of a new habit, followed by *range expansion* due to the competitive advantage provided by the new habit. Second, is the *range fragmentation* of the now wide-spread species, primarily due to vicariance of suitable habitat as a result of climate change, and subsequent *differentiation* of isolated populations in the habitat fragments due to increased pressure resultant from shrinking resources. This differentiation may take the form of the adaptation to a *new niche* in the current habitat (along any dimension, such as food source or nest location). It may also take the form of the development of a new *habit*, which may not only infer competitive advantage within the habitat refuge, but may well also free this new species (the second new species in Hall's proposed speciation cycle) to invade the expanding habitats outside of its original habitat, which at this stage is confined to the aforementioned islands. Hall (1972) suggests that such a speciation cycle may well explain the existence of the many superspecies that have members inhabiting a number of different habitats.

Speciation takes place when the genetic composition of demes (local populations) within a population differentiate to a degree which produces minimum diagnosable units (as defined by the Phylogenetic Species Concept, Cracraft 1983), or operational taxonomic units (as defined by the Phenetic Species Concept, Sneath & Sokal 1973), or where there is a breakdown of mate recognition systems (as defined by the Biological Species Concept, Paterson 1985; Mayr 1942). For genetic differentiation to occur, perturbation of the Hardy-Weinberg equilibrium frequency distribution of genes must take place (e.g. Stansfield 1983 as for the rest of this paragraph). Hardy-Weinberg conditions can be violated if new genes are introduced into a population through genetic mutations (e.g. transversions and translocations) *and* then selected for. If no selection acts on mutated genes, then the change will probably be cancelled out by back mutations. Alternatively, slight changes in the environment of one or both demes from the parental situation could lead to selection for specific traits, such that the frequency of the selected genes

increases in the deme. Random changes in gene frequencies occur constantly, but in large populations do not change the mean condition. However, in small populations, random fluctuations are not always countered, and they may become fixed, that is random genetic drift has taken place. The genetic composition of a small populations, especially those that have been through 'bottlenecks', will be determined by the sample of individuals remaining. This 'founding stock' may not be representative of the parental population (founder principle). All of these mechanisms, namely selection, random genetic drift and founder principle, act more quickly in a small population, and the last two are only affective in small populations. Isolation enhances the effects of these mechanisms, as genetic exchange with other demes may quickly neutralise the effects of mechanisms of founder principle and bottlenecks.

Consequently, most models of avifaunal speciation postulate spéciation in allopatry (e.g. Haffer 1969, 1997; Cracraft & Prum 1988 in South America; Cracraft 1986, 1994 in Australia; Hall & Moreau 1970; Diamond & Hamilton 1980; Crowe & Crowe 1982; Crowe & Kemp 1986; Fry 1986; Prigogine 1986; Mayr & O'Hara 1986; Fjeldså 1994; Roy *et al.* 1997 in Africa,). Note, however, that some studies have also put forward models of parapatric (discussed in Cracraft & Prum 1988; Haffer 1997) and sympatric speciation (e.g. Grant 1991). The main emphasis of studies of patterns of avifaunal speciation has been on the cause of allopatry. Isolation can be due to vicariance, that is the separation of the parental population into two or more demes, or by a successful long distance dispersal and establishment event. Vicariance mechanisms postulated include continental plate movements, marine intrusions, mountain formation, and river formation (e.g. Cracraft 1973; Crowe & Kemp 1986; see Haffer 1997 for a review of mechanisms postulated in South America). The vicariance mechanism postulated most widely is climate induced vegetation fluctuation (e.g. Chapin 1932; Moreau 1966; Diamond & Hamilton 1980; Crowe & Crowe 1982; Crowe & Kemp 1986 for African avifauna; Cracraft & Prum 1988 in South America; Cracraft 1986, 1994 for Australian avifauna; Haffer 1969, 1997 for Neotropical avifauna). The last was immortalized by Haffer's (1969) Pleistocene vegetation refugia study. More recently, Fjeldså and co-workers (Fjeldså 1994; Fjeldså & Lovett 1997; Fjeldså *et al.* 1997,) point out that climate-induced habitat fluctuations can affect speciation at all time scales, not just at the lengthy cycles of the Pleistocene, and

also on a very localised scale.

Causes of initial speciation events are difficult to investigate based on current distributional patterns. For instance, current contact zones of sister species cannot be assumed to reflect vicariance agents. Although contact zones may coincidentally be congruent with the vicariance event, they may also be situated at a more recently formed dispersal barrier. The contact zone may also simply represent a coincidental meeting place of sister species, the situation of which contact line is maintained by competition (e.g. Roy *et al.* 1997) or by genetic mechanisms (Mayr & O'Hara 1986), rather than constituting a physical barrier. Peaks of narrow endemics, disjunctions and highly congruent repetitive radiating patterns of species richness may support the location of habitat refugia identified by analysis of historical climate data (e.g. Diamond & Hamilton 1980; Mayr & O'Hara 1986). However, caution in such exercises is needed, as many studies infer the locations of refugia from current distributional patterns, and then go on to propose refugia as explanations of these current distributional patterns, which reasoning is circular (e.g. Jenkins 1992). Even the use of peaks in narrow endemism to support the location of habitat refugia identified by analysis of historical climate data can be tricky as the presence of concentrations of narrow endemics cannot conclusively prove the location of the speciation events that are suggested to have resulted in the development of narrow endemics. Particularly, if it is not known whether a species is a paleo- or neo-endemic, one cannot assume whether the species originated where it currently occurs (which is likely in the case of a neo-endemic) or whether the current restricted distribution is relictual in which case the species may well have originated elsewhere (in the case of a paleo-endemic). In addition, sampling bias may lead investigators to suggest the existence of refugia in well sampled areas (e.g Beven *et al.* 1984). Inadequate sampling may portray geographical features as barriers that the addition of new data refutes. For instance, in the Upper Guinea forests, the addition of new distributional data shows that physical barriers, such as rivers, valleys, and mountains, have probably played a minor role in determining patterns of species distribution (*contra* Kemp & Crowe 1986). In other cases, data mapped at the scale of this study seemed to support physical barriers, which more detailed field knowledge disproved. For example, based on one-degree scale of digital data generated by this study, it appeared that the Ruaha Rift

separated the distributions the superspecies pair of *Ploceus* [*olivaceiceps*] *olivaceiceps* and *P.* [*olivaceiceps*] *nicolli*. However, field knowledge shows that distribution of *P.* [*olivaceiceps*] *olivaceiceps* is, in fact, not limited by the Ruaha Rift (J. Fjeldså pers. comm.). However, despite these problems, cases do exist where a number of sister species have congruent contact zones that coincide with physical features (Mayr & O'Hara 1986). Some of the clearest examples are the dry river valleys and rift valleys in the *Brachystegia* avifauna of the Southern Savanna Subregion (*sensu* Benson *et al.* 1962; Benson & Irwin 1966; Crowe & Kemp 1986; see also results presented in this chapter).

The effect of historical climatic oscillations through vegetation fluctuations is likely to have had a much larger role to play in determining distributional patterns of the Afrotropical avifauna, as has been suggested by Diamond and Hamilton (1980), Crowe and Crowe (1982) and Fjeldså *et al.* (1997), than various other proposed barriers. Patterns of superspeciation support the 'refugium hypotheses' put forward by the aforementioned papers. Note, however, that Fjeldså's refugia (e.g. 1994; Fjeldså *et al.* 1997) are localised patches of climatic stability rather than large patches of climatic stability of the Pleistocene refuge theories.

5.5. Conclusions

Discrete avifaunal communities inhabit different portions of the Afrotropics. Each of these distinct avifaunas must be represented in a conservation scheme that aims to represent avifaunal diversity of the Afrotropics. Major subregions closely follow broad centres of endemism identified for phytochoria. Patterns of superspeciation show that, within larger avifaunas (subregions), patterns of species richness and narrow endemism are often related to historical factors. In many instances historical speciation events are likely to have been determined by vicariance through climate induced habitat changes, whether these climatic variations take place on the medium (e.g. Fjeldså 1994; Fjeldså *et al.* 1997) or long (Diamond & Hamilton 1980; Crowe & Crowe 1982) term. A prime example of such climatically induced patterns are the affinities between the Northeastern and Southwestern Subregions associated with the arid

corridor. This distributional pattern is well-supported by superspecies pairs. Formation of physical barriers, such as rivers or mountain ranges, are likely to have played only a minor role as vicariant speciation events in the Afrotropics. Such physical structures are more likely to have played a role in retarding relaxation of taxa out of vegetation refugia. It is often difficult to discern the possible effects of history and the current environment. For instance, the identification of the Disjunct District in the Guineo-Congolian Subregion, and the occurrence of a number of superspecies pairs in the two portions of the Disjunct District can be taken as evidence for a Cameroon-Gabon and a northeastern Congo basin (Ituri) refugium, which were alternatively separated by the invasion of savanna and the development of a Congo basin lake (e.g Crowe & Crowe 1982). However, data from Chapter 4 indicate substantial differences in productivity and intra-annual stability between the Disjunct District and the intervening Central District, such that these patterns of disjunction may be, at least in part, attributable to current patterns of carrying capacity rather than due to historical refugia. However, statistical analysis can never resolve this situation, partly because relevant palaeoecological data are insufficient, and partly because statistical analysis cannot differentiate between history and current patterns of redistribution (e.g. Fjeldså & Lovett 1997; Haffer 1997; Tuomisto & Ruokalainen 1997).

CHAPTER 6. Setting priorities for the conservation of Afrotropical birds

Summary

Efficiency (that is the number of areas needed to represent all species in a database) of near-minimum sets defined by complementarity analysis is influenced by the degree of nestedness in patterns of biotic distribution. Here nestedness refers both to the co-occurrence of narrow endemics, and to the coincidence of concentrations of narrow endemics with peaks of species richness. Where narrow endemics show a high degree of co-occurrence, few irreplaceable areas (that is grid cells selected by complementarity analysis to represent single-cell endemics) are needed, increasing flexibility and efficiency in the resultant near-minimum set. Where concentrations of narrow endemics coincide with peaks of species richness, irreplaceable grid cells simultaneously cater for large numbers of more widely distributed species, decreasing the total number of grid cells needed to represent all species in a database. The Guineo-Congolian Subregion provides a good example of nested patterns, where localised areas of stability (which probably act through both the elevation of current carrying capacity and promotion of speciation rates during climatic vicissitudes) are characterised by both co-occurrence of narrow endemics and coincidence of concentrations of narrow endemics with peaks of species richness. The Northeastern Subregion (which encompasses the Sahel and the Horn of Africa) provides an example of non-nested patterns where narrow endemics are dispersed throughout the Ethiopian Highlands and adjacent Somalia-Masai lowlands, resulting in a relatively large number of grid cells being needed to represent relatively few species.

A biogeographical approach to complementarity analyses (that is the identification of a near-minimum set for each avifaunal subregion based on bird species strongly associated with that subregion) is slightly less efficient than a sub-continental (subSaharan Africa) approach. A biogeographical approach requires 4.8% more grid cells to represent all species once, and 9.7% to represent all species five times, than does a sub-continental approach. However, a biogeographical approach helps to

prevent the conservation of species in marginal areas (that is at the edge of their ranges), which is deemed undesirable as such areas are often dynamic in both composition and location.

The a priori *selection of grid cells to represent Red Data species does not incur a marked cost (in terms of near-minimum set size), and may prove to be a useful strategy to ensure that grid cells that represent RD species achieve high priority within a near-minimum set to represent Afrotropical birds.*

6.1. Introduction

Conservation of birds is important due to their flagship status (e.g. ICBP 1992; Collar *et al.* 1994). The charisma of birds has long afforded them popular support, most aptly demonstrated by the fact that the Royal Society for Bird Protection constitutes roughly 1.5% of the population of Britain (e.g. Williams *et al.* 1996a). This attraction among both amateurs and scientists has resulted in birds being probably the best studied higher taxon. The comparative wealth of distributional and taxonomic (and even phylogenetic) data for birds (e.g. Williams *et al.* 1996a and references therein) allows their use in the development of protocols that can be applied to less well-studied groups (e.g. Turpie 1995). Birds are also powerful players in the economic market place, generating large amounts of revenue, particularly from bird watching and hunting (Jacquemot & Filion 1987).

A regional approach to defining conservation priorities for birds is taken in this study to ensure biologically meaningful definitions of endemism and rarity, and to improve efficiency. A purely political definition of endemism, whilst pragmatic and necessary to infer national responsibility and action (Drinkrow & Cherry 1995; L. Fishpool in litt.), can result in narrow endemics not being identified as priorities (see example cited in Chapter 3). In addition, when a purely political perspective is taken, the assignment of endemic status can be biologically meaningless. Many tropical species of various taxa extend marginally into South Africa, known as the subtropical subtraction effect (e.g. Gelderblom *et al.* 1995). When South Africa alone is viewed, these species appear rare and in need of conservation action, when in fact they are common and not under threat to the north of the country's borders (e.g. Four-toed Elephant Shrew *Petrodromus tetradactylus*, Wahlberg's Epauletted Fruit Bat *Epomophorus wahlbergi*,

and Serval *Felis serval*; see Skinner & Smithers 1990 for distributional data for these species). If the focus of a study is too narrow, resultant priorities may be inefficient from a regional point of view. For example, if a complementary set of grid cells is identified to represent all plants that occur in KwaZulu-Natal, South Africa, considerably more grid cells are needed than if a complementary set that represent these plant species is identified on a larger scale (for South Africa as a whole) (Rebelo 1997).

This study aims to take a sub-continental approach to identifying local regions (grid cells) important for conserving terrestrial resident Afrotropical birds within a biogeographical framework. The most efficient combination of grid cells which represents all terrestrial resident Afrotropical bird species at least once is identified by near-minimum set analysis. Near-minimum sets are identified for each avifaunal subregion (as identified in Chapter 5) based on its subregion-associated species. Patterns of species richness and narrow endemism (as measured by indices of range-size rarity) within avifaunal subregions are determined for interpretative purposes. High priority grid cells are identified as near-minimum sets within each biogeographical subregion. Grid cells identified are not suggested as sites for formal protection, but rather represent a starting point for conservation studies. Such studies would have to ground-truth results, check for population viability of the target species (that is those species that the grid cell has been chosen to represent) and suggest conservation plans for the target species. Conservation action need not take the form of formal protection and may include local community projects or aim to address macro-economic policy (e.g. Fjeldså & Rahbek in press).

6.2. Methods

6.2.1. Database

Birds occurring in the Afrotropics fall into a number of life history categories. Firstly, birds can be terrestrial, aquatic (dependent on non-marine aquatic biotopes for feeding, breeding *sensu* Guillet & Crowe 1985, and/or roosting) or marine. Waterbirds (aquatic species) have been shown to have different distributional patterns to those of terrestrial species (Moreau 1966; Guillet & Crowe 1985). Seabirds are affected by different ecological and exploitative process to either terrestrial or waterbird species, and so

their conservation should be considered separately (J. Cooper pers. comm.). Secondly, species can be resident (sedentary or exhibiting localised movement over short distances), intra-African migrants or inter-African migrants, which come chiefly from the Palaearctic. Intra-African migrants were not separated out from resident species endemic to the Afrotropics, as insufficient data are currently available to enable rigorous definition of movements and mapping of movement routes and breeding sites of such species. Most Palaearctic migrants are non-breeding, but 15 species have local populations that breed in the Afrotropics (e.g. *Egretta garzetta*, *Plegadis falcinellus*, and *Sterna albifrons*, see Chapter 2 for further discussion). In some of these cases, the resident and migrant populations represent separate subspecies (e.g. *S. a. guineae* and *albifrons*) such that conservation of the resident populations could be viewed as important. However, separating out records for resident populations from records for migrants proved difficult and these 15 species have been classified as Palaearctic migrants. Lastly, resident species can have their entire global range restricted to the Afrotropics (termed 'Afrotropical endemics' in this study), be centred in the Afrotropics, but extending to some degree beyond the region, or be centred outside of the Afrotropics, but extending to some degree into the Afrotropics. Species centred in the Afrotropics that extend some distance beyond the bounds of the Afrotropics to include north Africa (e.g. Moreau 1966; followed by Brown *et al.* 1982), southern Arabia (e.g. IUCN 1986; Maclean 1990; Dowsett & Forbes-Watson 1993), Madagascar or the islands of Comoro, Aldabara, Seychelles and Socotra (P.A.R. Hockey pers. comm.) should be considered for conservation action within the Afrotropics. Species that have distributional ranges centred outside of the Afrotropics are not the prime focus for conservation action that is planned within the Afrotropics, and should rather be *actively* conserved in areas where their ranges are centred. Combinations of these life history and distributional traits form six classes (see ◯ numbers in Table 6.1.), namely terrestrial species that have ranges centred on the Afrotropics (1484 species), nonendemic terrestrial residents (50 species), terrestrial migrants (112 species), waterbirds that breed in the Afrotropics (154 species), non-breeding migrant waterbirds (74 species), and all seabirds (37 species).

Species in each of the six different categories will require different conservation approaches. For instance, many seabirds require global efforts aimed at reducing deaths of breeding adults near important

breeding colony sites caused by long-line fishery associated activity (Brothers 1991) and other effects of fisheries, such as entanglement in dumped gear and refuse (Ryan 1991). Migrants require site-based protection of their breeding and wintering ranges, as well as some form of protection of important stop-over sites and the individuals in transit (Biber & Salathe 1991). Unfortunately, insufficient data and time were available to divide broad ranges of migrants into passage, stopover and wintering records. Identification of priority sites for the conservation of Palaearctic migrants is then probably best left to BirdLife International's Important Bird Area (IBA) approach (L. Fishpool in litt.). This is especially so for waterbirds for which abundance data amassed by the International Waterfowl and Wetlands Research Bureau (e.g. Dodman & Taylor 1995) are a great improvement over the presence-only data available to this study. Consequently no attempt is made in this study to highlight possible areas for conservation action for seabirds, migrants, waterbirds, or terrestrial residents that have ranges which are centered outside of the Afrotropics. This leaves the 1484 terrestrial residents that have a global distributional range centred in the Afrotropics (termed Afrotropical species; coded as 'ER' in Table 6.1), which species are considered in this study.

Table 6.1. Life history and distributional categories used to derive analysis groupings (ER = distribution centred in Afrotropical region, NE= distribution centred outside the Afrotropics, BP = Palaearctic migrants to the Afrotropics that have local breeding populations within the Afrotropics, PM = Palaearctic migrants, and MM = migrants from Madagascar)

		Terrestrial		Waterbirds		Seabirds	
Breeding residents	ER	1484	①	104	154 ④	4	
	NE	50	②	50		13	37 ⑥
Migrants	BP	15		12		7	
	PM	96	112 ③	61	74 ⑤	12	
	MM	1		1		1	

6.2.2. Priority analyses

6.2.2.1. CRITERIA FOR BIOLOGICAL CONSERVATION

Criteria used to evaluated conservation value of grid cells (see Chapter 2 for a description of grid cell system used to digitise distributional data) for the conservation of Afrotropical bird species are total

richness of Afrotropical species, and three measures of threat, namely richness of Red Data (RD) species, richness of rare-quartile species and richness of range-restricted species. Species richness is a popular definition of diversity (Noss 1990), which approximates character diversity for large databases (Williams *et al.* 1994). It also ensures maximum representation of species diversity, if species richness is accepted as an approximation of diversity, and if threat is unpredictable (Williams *et al.* 1996a). However, if some species are more at risk of becoming extinct over the short term, aiming conservation efforts at maximum species richness may not maximise total diversity conserved over the long term (e.g. Williams *et al.* 1996a). This is particularly so if areas rich in species do not coincide with areas containing species experiencing greatest threat of extinction (see Williams *et al.* 1996a for discussion). It has been argued that many species contributing to the high species tallies of species richness hotspots are widespread, highly adaptable and under no immediate threat, and thus are not of great conservation concern (Thirgood & Heath 1994; Fjeldså 1994). Diamond (1985) suggested that the aim of reserve systems should not be representation of maximum species richness, but representation of those species that are likely to become extinct in the absence of such 'safe havens'. In some situations, aiming conservation at maximising species richness over the short term may, in fact, work against maximising the number of species conserved over the long term if resources are ploughed into areas containing many 'healthy' species whilst neglecting those at risk of being lost. Threat is most commonly identified by the classification of species according to RD criteria. RD classification was applied to birds in Africa by Collar *et al.* (1994). A total of 91 Afrotropical bird species are classified as RD species, of which seven are identified as critical, 15 as endangered, and 69 as vulnerable (Appendix 6.1). Rarity can also give an indication of threat. One of the more commonly measured aspects rarity is range-size (e.g. Terborgh & Winter 1983; see Rabinowitz *et al.* 1986 for a description of different types of rarity, and Gaston 1994 for a critique of the Rabinowitz approach). Range-size rarity can be measured as a discontinuous or continuous variable (see Gaston 1994 for discussion). The rare-quartile, a frequently used discontinuous measure, gives greatest weight to the most restricted species (Gaston 1994). However, discontinuous definitions tend to be arbitrary and assemblages usually compromise species exhibiting a variety of range-sizes, which seldom separate into discrete groupings (Gaston 1994). Consequently, continuous measures are often

used, such as weighted richness by inverse range-size (Csuti *et al.* 1997) which, although dominated by rare species, considers all species (e.g. Williams *et al.* 1996a).

6.2.2.2. TECHNIQUES FOR SETTING CONSERVATION PRIORITIES

Methods used to apply criteria to develop priority listings of areas (or grid cells in this study) for conservation attention were dominated by once-off ranking procedures prior to the last decade (e.g. Margules *et al.* 1988). However, such methods have been widely shown to be inefficient compared with complementarity techniques (e.g. Margules *et al.* 1991; Lombard 1995b; Williams *et al.* 1996a; Kershaw *et al.* 1994). Once-off ranking procedures usually result in some species being afforded repeated representation, whereas many others are not represented at all (Williams *et al.* 1996a). Once-off ranking procedures, such as hotspot analysis, may be of some value, however, in that they provide guidance for evaluating near-minimum sets derived from complementarity analysis (Turpie 1995). Complementarity algorithms ensure (near) minimum number of areas needed to represent all species, and maximum number of species representations per specified number of areas (Williams *et al.* 1996a).

The near-minimum set approach was also preferred to simply siting one priority area in each biogeographical subregion and one in each transitional area as suggested for marine systems by Hockey and Branch (1994). Their approach must assume highly nested patterns of species distribution. Nestedness refers to the situation in which any species in smaller faunas also occur in all larger faunas (Cutler 1991; Wright & Reeves 1992). This pattern, however, as Cutler (1991) has suggested, is seldom perfect, such that it is not surprising that selection of only one priority area per biogeographical zone and one per biogeographical transition has been shown to be inadequate to represent the full biota of regions (J.K. Turpie unpublished data). Turpie & Crowe (1994) offer the more useful suggestion that conservation of representative taxa for each biogeographical subregion and province be a minimum requirement, but this also does not ensure full representation of the total fauna or flora of each biogeographical region. L. Fishpool (in litt.) has been among the first to specify the need for full representation of each fauna or flora in each biogeographical region and suggest that this be achieved through implementation of complementarily principles.

Although heuristic algorithms provide suboptimal results (Underhill 1994), a number of heuristic algorithms with redundancy back-checks (Williams *et al.* 1996a; Pressey *et al.* 1997) have been shown to approximate efficiency levels of more rigorous linear-programming branch-and-bound (such as those used by Cocks & Baird 1989; Willis *et al.* 1996) and maximum coverage techniques (such as those used by Church *et al.* 1996) (e.g. Csuti *et al.* 1997; Pressey *et al.* 1997). In addition, the latter two methods are often intractable for large problems, whereas heuristic algorithms allow fast, interactive analysis (Pressey *et al.* 1996). Although it is difficult to determine *a priori* which combinations of rules in a heuristic algorithm will offer solutions closest to the optimum in a specific situation (Pressey *et al.* 1997), a few general guidelines can be tentatively assumed based on comparative studies. For instance, if the goal is to *minimise the number of areas* needed to represent a biota, where number of areas is a surrogate for cost (Williams *et al.* 1996a), then rarity-based algorithms are relatively efficient (Csuti *et al.* 1997). If the goal is to determine the *maximum number of species that can be represented* in a set number of areas (a maximum coverage problem), then richness-based algorithms fare best (Csuti *et al.* 1997). A compromise can be achieved using a progressive rarity algorithm (Margules *et al.* 1988) with resequencing of selected sites by complementary species richness (Csuti *et al.* 1997). The aim of this study is to represent Afrotropical bird diversity in the most efficient manner possible (that is in the minimum number of grid cells possible), as each conservation project aimed at species or habitat protection represents an opportunity cost for other conservation initiatives and research needs.

Irrespective of the method used to prioritise areas according to the chosen criteria, comparisons across distinct biogeographical zones may be inappropriate (e.g. Emanuel *et al.* 1992; Turpie & Crowe 1994; Gelderblom *et al.* 1995; Turpie 1995). This is particularly so in the diverse region of subSaharan Africa (see also Chapter 1). In order to be able to conduct conservation prioritisation analyses within biogeographical zones, those species 'belonging' to various biogeographical subregions (as identified in Chapter 5; Fig. 5.3a) have to be identified. Terrestrial Afrotropical bird species that are more than 50% restricted to one of the six avifaunal subregions defined in Chapter 5 are termed subregion-associated species. The rationale behind a 50% cut-off follows that of the Braun-Blanquet floristic association method as applied by Westhoff & van der Maarel (1973) which suggests that any species which has more

than half of its range restricted to a particular subregion, is likely to be more strongly associated with that subregion than any other.

For total species richness and narrow endemism (measured as both range-size rarity or rare-quartile richness) hotspot analyses are performed for each subregion based on their subregion-associated species. Hotspots are identified as the highest scoring 5% of grid cells in the database. The 5% criterion is arbitrary, but frequently used, cut-off level (e.g. Prendergast *et al.* 1993b; Lombard 1995a; Williams *et al.* 1996a). Complementarity analysis are performed with a progressive rarity algorithm with a redundancy check and re-ordering of selected sites on complementary species richness within each subregion based on their subregion-associated species. Near-minimum sets were checked to ensure that the 206 species (of the 1484 Afrotropical species, i.e. 13.9%) that are not defined as subregion-associated are also catered for (additional areas identified by complementarity if necessary).

In order to investigate the possible effects of a subregional approach to the identification of complementary priority areas on efficiency (that is the number of grid cells needed to represent all bird species a specified number of times), the total number of grid cells identified in all six subregional near-minimum sets is compared to the number of grid cells identified if the analysis is run for the whole Afrotropical region. Both sets of analyses are based on subregion-associated species only (n = 1231) in order to keep the number of species involved constant. These comparisons were made between sets identified to represent all subregion-associated species once, three and five times, respectively. Repeat representations of species, where possible (for species that occur in more than one, three or five grid cells, respectively), can be included as an algorithm constraint to increase the chance of viable populations being conserved (e.g. Kershaw *et al.* 1994; Lombard *et al.* 1995; Williams *et al.* 1996a).

For analyses using Red Data species as the criterion for assigning priority, the Afrotropical sub-continent was considered as a whole. Overall patterns and hotspots of Red Data species were plotted. A complementary set was determined to represent all RD species once. This set was used as an *a priori* selection constraint in an complementary analysis of the remaining 1114 (of the 1230) subregion-

associated species. This was done in order to evaluate the effect of imposing the *a priori* selection of grid cells to represent RD species on the efficiency of the algorithm's performance.

All analyses are performed using WORLDMAP software (ver. 4.17.01, Williams 1997).

6.3. Results

6.3.1. Northeastern Subregion

Patterns of species richness are concentrated in the Somali-Masai lowlands (Figs. 6.1a & b), whereas narrow endemism (measured as range-size rarity or rare-quartile) is concentrated in the Ethiopian Highlands (Figs. 6.1c – e). A large proportion of the near-minimum set constitute irreplaceable grid cells (8 out of 17, or 47 %; Table 6.2; Fig. 6.1f). Four irreplaceable grid cells occur in the lowlands and are selected to represent one range-restricted species each, namely *Mirafra williamsi*, *Mirafra degodiensis*, *Laniarius liberatus* and *Mirafra ashi*. Coincidence of range-restricted species in the highlands is also fairly low, resulting in a further three irreplaceable grid cells being identified. One irreplaceable grid cell identified in the highlands does represent a number of range-restricted species (e.g. *Hirundo megaensis*, *Cercomela dubia*, and *Serinus ankoberensis*)

6.3.2. Northern Savanna Subregion

Species richness and narrow endemism (both indices of range-size, namely the rare-quartile and range-size rarity) are concentrated in the broad band of Sudanian woodland which runs northwest to southeast (Figs. 6.2a – e). Peaks of both species richness and narrow endemism occur in the region of the Sudd and woodland-savanna transition to the south thereof (Figs. 6.2b & d). Richness of narrow endemics is highest in the Bameda Highlands, continuing to the northeast and northwest thereof. Other mountains of West Africa also score highly. The importance of the Niger Inundation and Lake Chad are clear. Additional narrow endemism peaks are associated with forest-savanna transitions in the Upper Guinea, and in the Ubangi-Uelle Savanna.

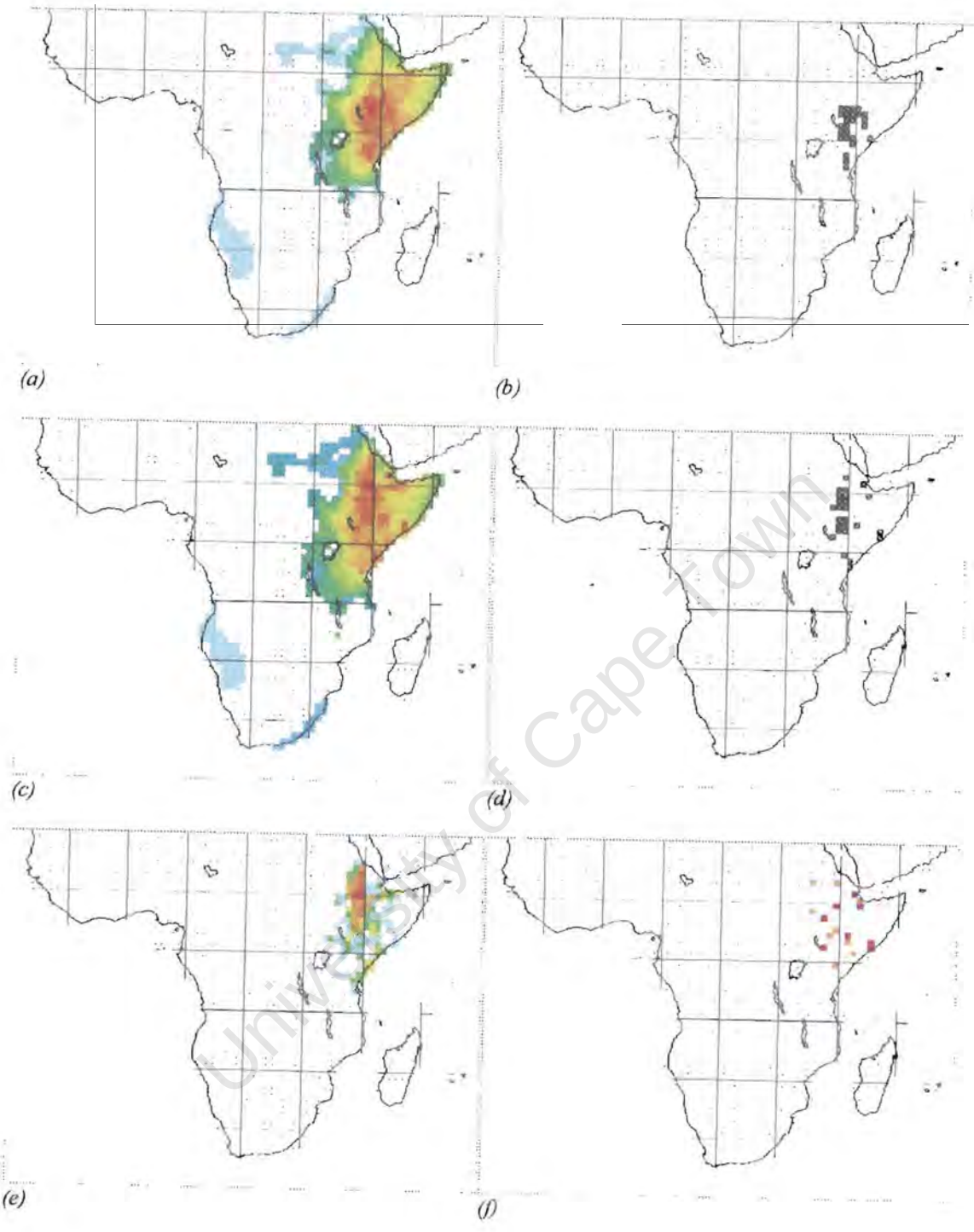

Figure 6.1. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 153 species associated with the **Northeastern Subregion**. Irreplaceable grid cells are shown in red and flexible choices in yellow.

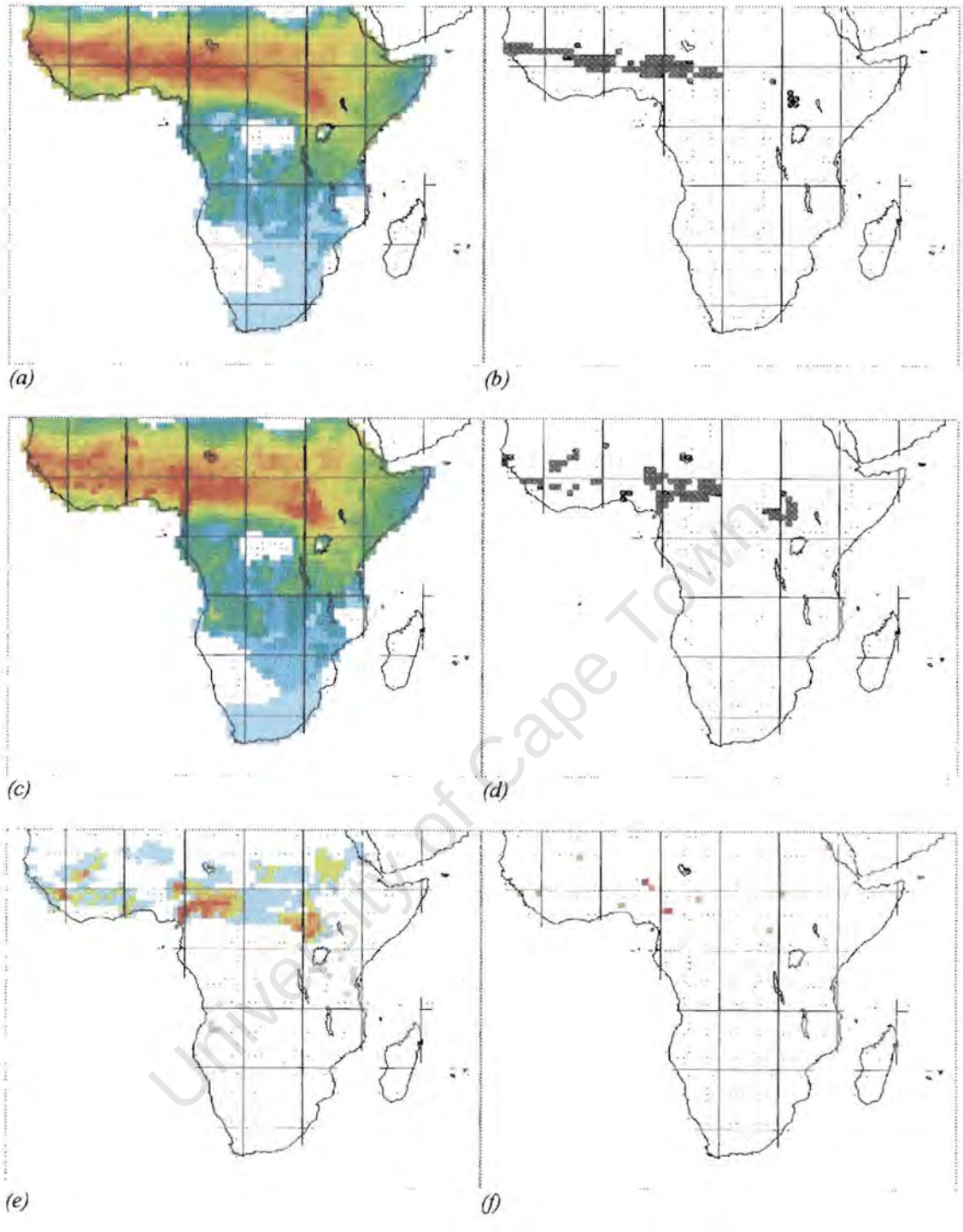

Figure 6.2. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 149 species associated with the **North Savanna Subregion**. Irreplaceable grid cells are shown in red and flexible choices in yellow.

The near-minimum set of 13 has 2 irreplaceable grid cells, which are selected to represent *Vidua raricola* and *V. larvaticola* (both single grid cell endemics), which parasitize *Lagonosticta rara* and *Lagonosticta larvata* respectively. Both of the host species are considerably more widespread than their respective parasites. The narrow distribution of these two parasites was vetted with recent data from Dowsett & Forbes-Watson (1993).

6.3.3. Southern Savanna Subregion

Species richness is centred in the diverse *Brachystegia* woodlands of Zambia and Malawi, with isolated peaks on the Angolan Escarpment, the Eastern Arc Mountains of Tanzania, and Chimanimani Mountains of eastern Zimbabwe and western Mozambique (Figs. 6.3a & b). Narrow endemism (both measures) is concentrated on the mountains from the southern Kenya, through the Eastern Arc, and south to the Chimanimanis, and to the west on the Manika Plateau in the southeast of the Democratic Republic of Congo, and along the Angolan Escarpment (Figs. 6.3c - e). There is also a peak of narrow endemism in the coastal forest of South Africa. Near-minimum grid cells closely follow the pattern of narrow endemism hotspots, with the 10 irreplaceable grid cells primarily occurring in the mountains, with two coastal grid cells in the Benguela Plain (*Mirafra naevia*) and Arabouko-Sokoke forest, Kenya (*Anthus sokokensis* and *Ploceus golandi*), respectively (Fig. 6.3f). A further six lowland grid cells are selected, two at the coast to represent seven species of the Tongo-Pondoland mosaic (e.g. *Glaucidium capense*, *Apalis ruddi*, and *Nectarinia neergaardi*) and the very restricted *Batis reichenowi*, respectively. Two of the inland lowland priority grid cells represent species of the dry Acacia savanna south of lake Victoria (*Francolinus rufopictus* and *Histurgops rufcauda*). One falls in the Tuli block (*Francolinus swainsonii* and *Tockus bradfieldi*) and one in the *Brachystegia* woodland (*Lybius chaplini*, *Cisticola melanurus*, and *Ploceus angolensis*).

6.3.4. Guineo-Congolian Subregion

Species richness and narrow endemism (both measures) overall patterns and hotspots highlight the Albertine mountain-Ituri lowland complex, the Cameroon highland-Gabon lowland and West African

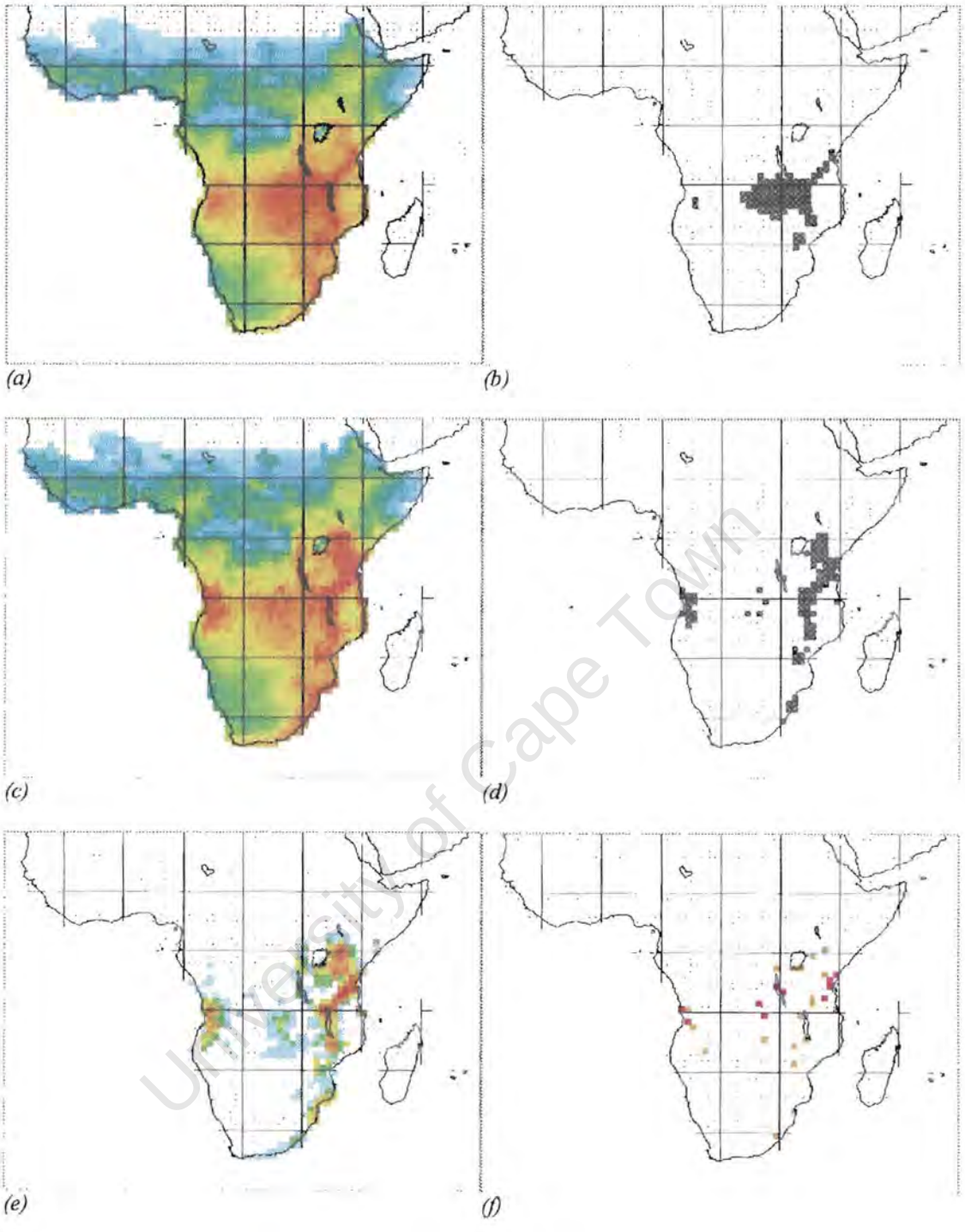

Figure 6.3. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 409 species associated with the **Southern Savanna Subregion**. Irreplaceable grid cells are shown in red and flexible choices in yellow.

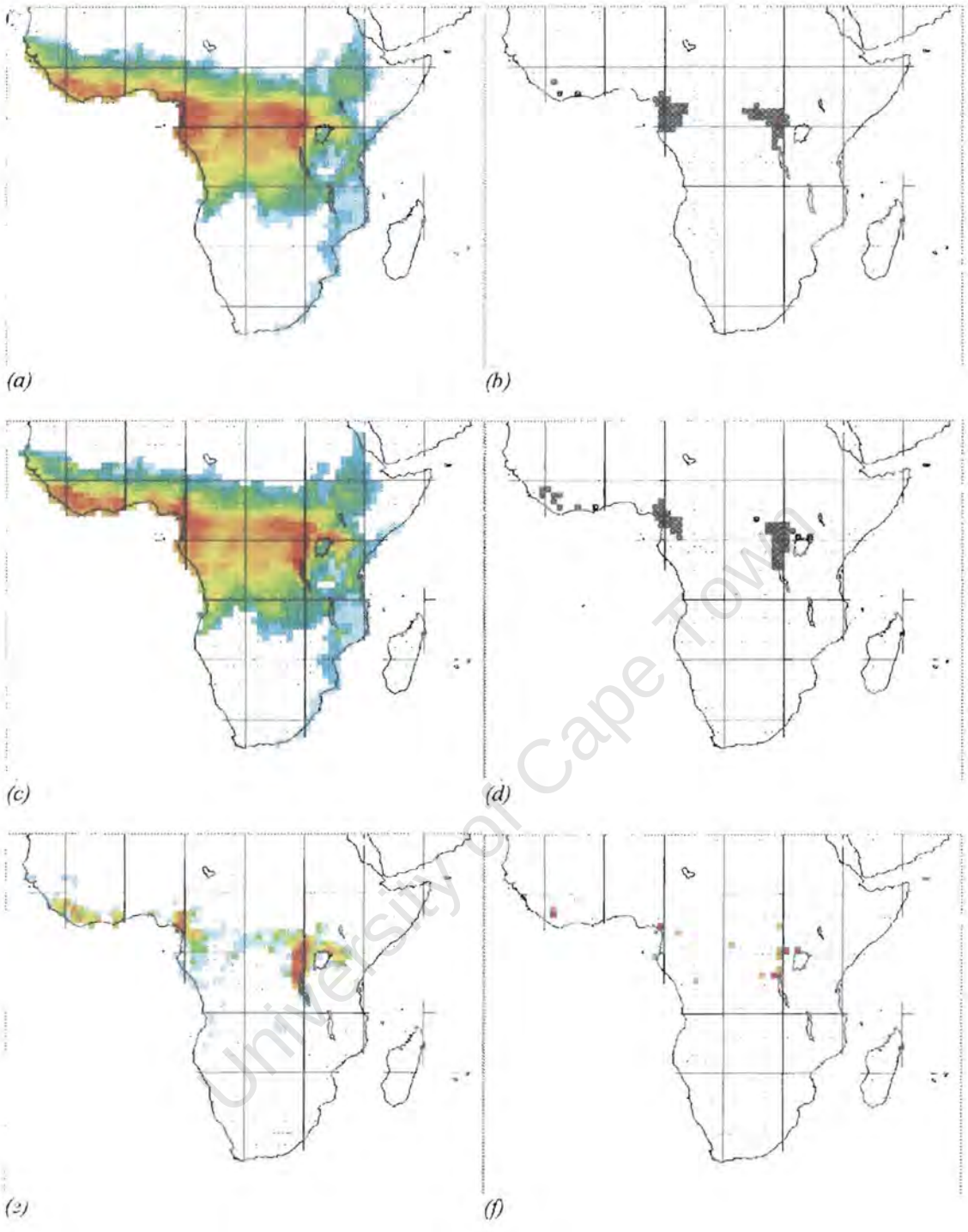

Figure 6.4. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 380 species associated with the **Guineo-Congolian Subregion**. Irreplaceable grid cells are shown in red and flexible choices in yellow.

mountains (Figs 6.4a – e). The near-minimum set identifies five irreplaceable grid cells and a further 12 that are flexible to varying degrees (Fig. 6.4f). Near-minimum set areas are again mainly situated in the vicinity of the three complexes outlined above. An additional grid cell is situated in the forest-savanna mosaic south of Brazzaville to represent the highly restricted *Cossypha heinrichi*, which only occurs in two other grid cells. Another priority grid cell is selected in the centre of the Congo to represent the three species restricted to the basin *Afropavo congensis*, *Apalis goslingi*, and *Nectarinia congensis*. This is a more flexible choice with a further five grid cells which contain all three of these species (Appendix 6.2). Another priority grid cell is located near the Ituri forest to represent *Psalidoprocne chalybea* and *Turdoides tenebrosus*. A further 12 grid cells could conserve both of these species.

6.3.5. Southwestern subregion

Species richness is concentrated in the Karoo and an area of high species replacement (see Chapter 5) between the western Kalahari and eastern Namib (Fig. 6.5a & b). Narrow endemism (both measures) is concentrated in the Cape Fold Mountains (e.g. *Turnix hottentota*, *Chaetops frenatus*, and *Serinus leucopterus*), extending east to Drakensberg-Lesotho Highland system (e.g. *Chaetops aurantius*, *Mirafra cheniana*, and *Serinus symonsi*) and north into the Namib coast (*Certhilauda erythrochlamys* and *C. barlowi*) and adjacent hills (*Namibornis herero*) and plateau (*Serinus leucolaema*) (Fig. 6.5c – e). No irreplaceable grid cells are identified in the near-minimum set (Fig 6.5f).

Table 6.2. Number of grid cells per subregion (Area), total number of subregion-associated species (Tot. Rich), Tot. Rich relative to Area (Rel. Rich), size of the near-minimum set (Set Size), Set Size as a proportion of the area of the subregion (Rel. Set Size - Area), Set size as a proportion of the number of subregion-associated species it had to represent (Rel. Set Size – Tot. Rich); number of irreplaceable grid cells in the near-minimum set (Irrep.), proportion of the near-minimum set which is irreplaceable (Rel. Irrep.)

Subregion	Area	Tot. Rich.	Rel. Rich.	Set Size	Rel. Set Size-Area	Rel. Set Size-Tot. Rich	Irrep.	Rel. Irrep.
Northeastern	162	153	0.94	17	0.10	0.11	8	0.47
Northern Savanna	552	149	0.27	13	0.02	0.09	2	0.15
Southern Savanna	467	409	0.87	29	0.06	0.07	10	0.34
Guineo-Congolian	319	380	1.19	17	0.05	0.04	5	0.29
Southwestern	228	127	0.56	10	0.04	0.08	0	0.00
Northern Arid	211	24	0.11	6	0.03	0.25	3	0.50

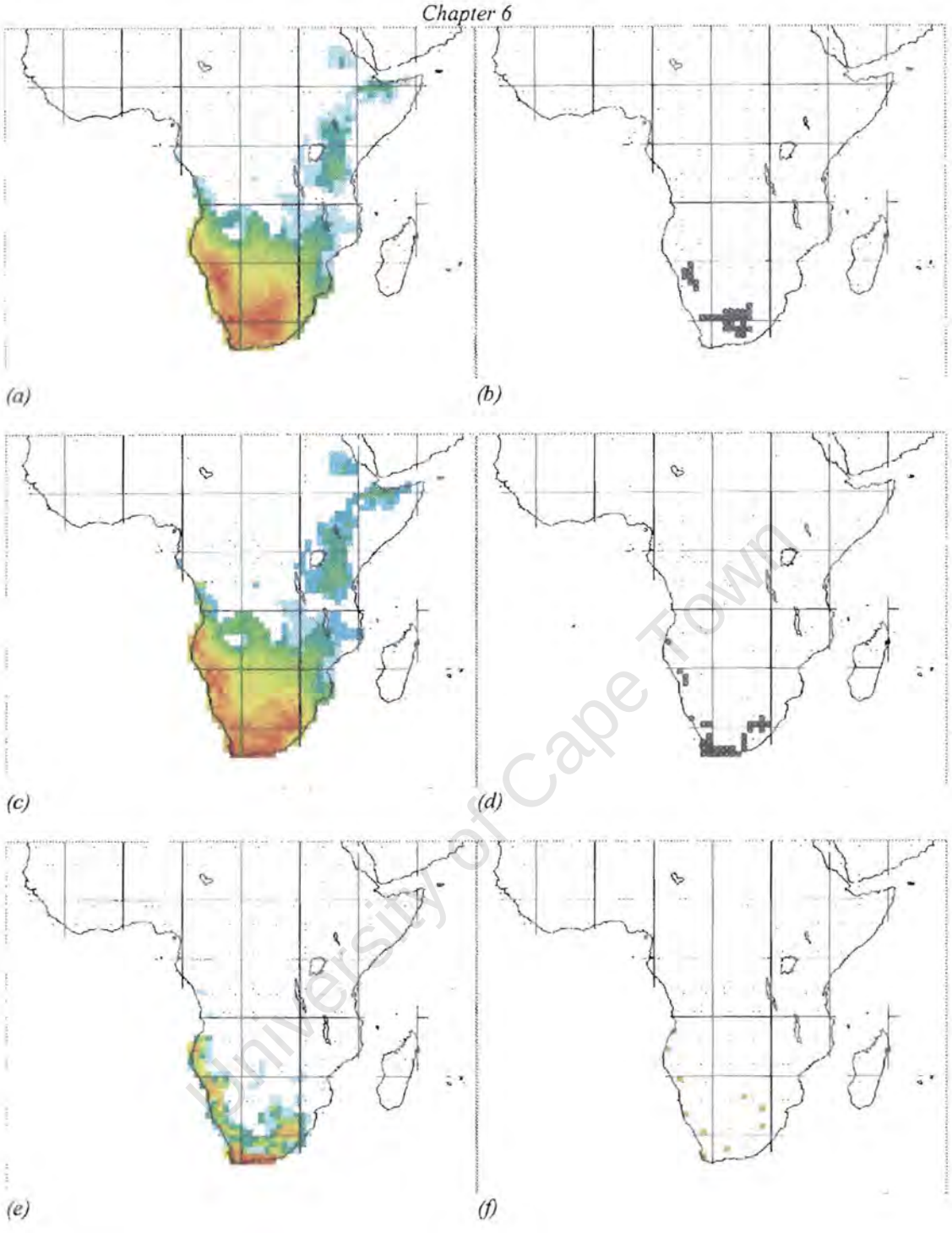

Figure 6.5. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 127 species associated with the **Southwestern Subregion**. Irreplaceable grid cells are shown in red and flexible chioces in yellow.

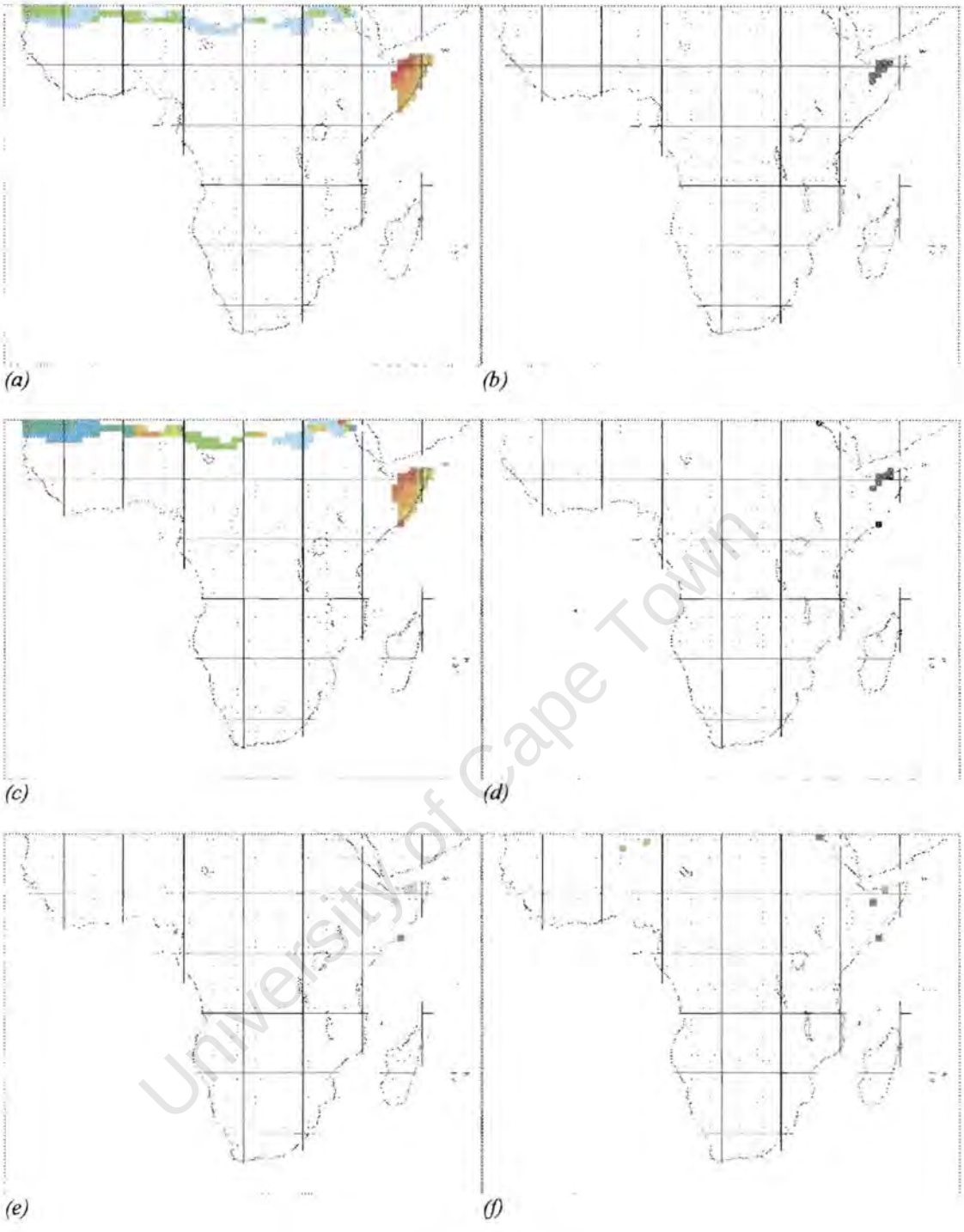

Figure 6.6. Species richness patterns (a) and hotspots (b), narrow endemism patterns (c) and hotspots (d), rare-quartile richness (e), and near-minimum set (f) for the 24 species associated with the **Northern Arid Subregion**. Irreplaceable grid cells are shown in red and flexible choices in yellow.

6.3.6. Northern Arid Subregion

This species-poor subregion (24 subregion-associated species; Table 6.2) has a large number of range-restricted species, most of which occur in Somalia from the coast inland to the Haud (*Dendropicos namaquas* and *Batis perkeo*). This is demonstrated by the fact that half of the near-minimum set constitutes irreplaceable grid cells (Table 6.2). Noteworthy species richness peaks occur in the Nugal Depression and mountains just to the north thereof (Warsengalia) (*Laniarius funebris* and *Monticola rufocinereus*) (Fig. 6.6a & b). Patterns of species richness and narrow endemism (both measures) are similar (Fig. 6.6a – d).

6.3.7. Relative efficiency of subregional near-minimum sets

The near-minimum set run to represent all subregion-associated species on a sub-continental scale (i.e. considering the whole of subSaharan Africa) identified 79 grid cells to represent all 1230 subregion-associated species once (Fig. 6.7), and 209, and 331 grid cells respectively to represent all species at least three and five times (Table 6.3). Individual subregional near-minimum sets identified a combined score of 89 grid cells for a single representation per species, and 226 and 363 grid cells for at least three and five representations per species, respectively.

Table 6.3. Near-minimum sets of grid cells derived from complementarity analyses, indication the ration of irreplaceable grid cells (Irrep.) and flexible grid cells (Flex) and the proportion of the set that is irreplaceable (% Irrep).

No of representations per spp.	*Sub-continent as a whole*	*Sum of sets for individual subregions*
1	79	89
Irrep. : Flex (% Irrep.)	25 : 54 (31.6)	25 : 64 (31.3%)
3	209	226
Irrep. : Flex (% Irrep.)	87 : 122 (41.6%)	89 : 137 (39.4%)
5	331	363
Irrep. : Flex (% Irrep.)	171 : 282 (51.7%)	179 : 184 (49.3%)

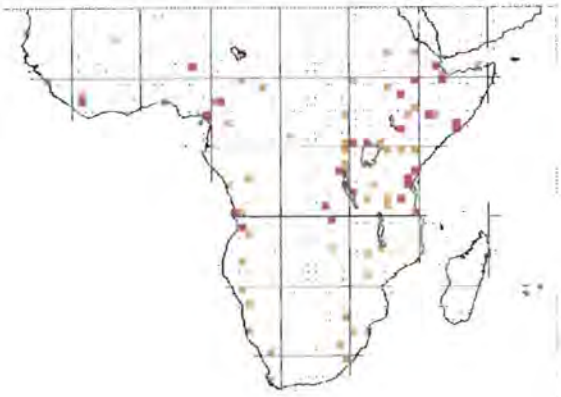

Figure 6.7. Near minimum set that represents all 1230 subregion-associated species at least once. Irreplaceable grid cells are shown in red and flexible choices in yellow.

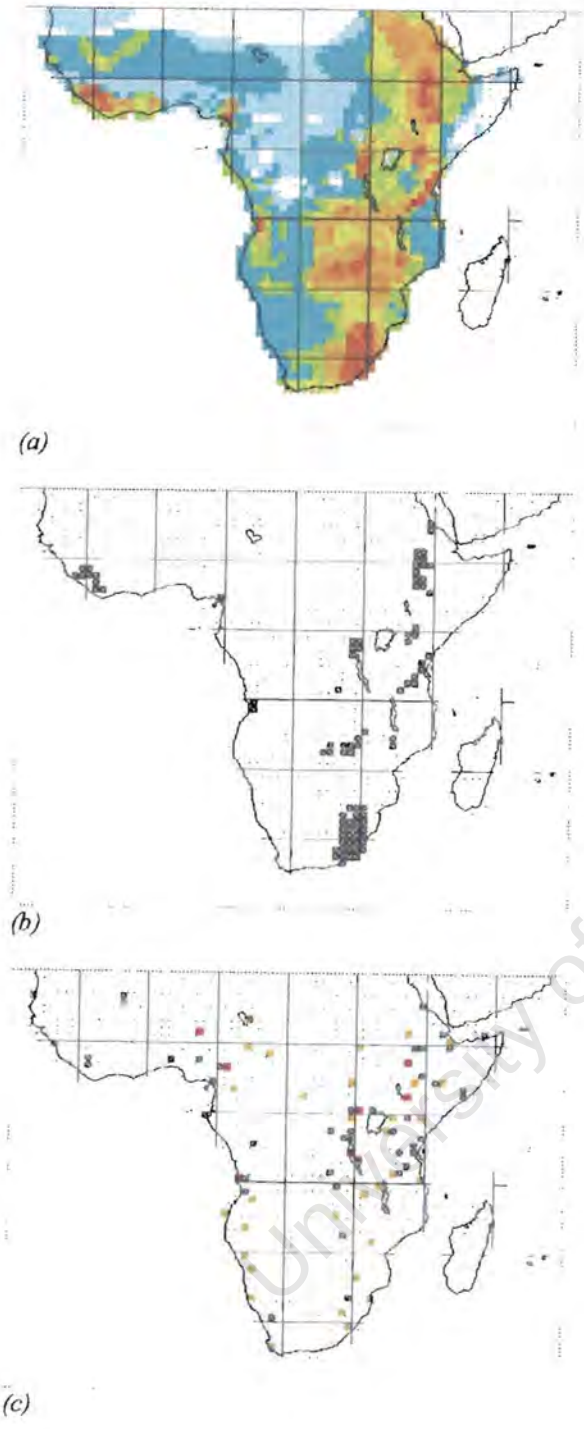

Figure 6.8. Species richness patterns (a) and hotspots (b) for the 116 Afrotropical RDB species. Near minimum set to represent all 1230 subregion-associated species with RDB species selected a priori (grey dots) (c). Irreplaceable grid cells are shown in red and flexible choices in yellow.

Identifying priority grid cells on a subregional basis is slightly less efficient than identifying priority grid cells on an sub-continental basis. Differences between the number of grid cells identified by the respective approaches range from 10 (ca. 4.8%) grid cells for a single representation per species to 32 (ca. 9.7%) grid cells for representation of species 5 times.

6.3.8. Red Data species

RD species occur throughout the Afrotropics (Fig 6.8a), but are concentrated in the mountains from Ethiopian to South Africa (Fig 6.8b). If complementary areas chosen to represent RD species are selected a priori (41 grid cells) before complementary analysis is run on the remaining 1114 of the 1230 subregion-associated species, a total of 85 grid cells are needed to represent all subregion-associated species at least once (Fig 6.8c).

6.4. Discussion

The size of a near-minimum set (that is the number of grid cells) relative to the total number of subregion-associated species for the subregion (i.e. Rel. Set Size – Tot. Rich.) gives an indication of how nested patterns of species richness are and of the extent of co-occurrence of narrowly endemic species (specifically single-cell endemics). The smaller the ratio of Set Size to total species richness for a subregion (i.e. the value of 'Rel. Set Size – Tot Rich'), the more efficiently the complementarity algorithm was able to situate priority grid cells, representing more species in fewer grid cells. This necessarily implies a greater coincidence of single-cell endemics (which species require irreplaceable grid cells) with each other and with peaks of species richness (such that irreplaceable grid cells also represent high total numbers of species and not just single-cell endemics). This can be illustrated by a comparison of patterns of species richness and narrow endemism and priority results for the Guineo-Congolian Subregion (Fig. 6.4a-f, Table 6.2) with the Northeastern Subregion (Fig. 6.1a-f, Table 6.2). In the Guineo-Gongolian Subregion, peaks of narrow endemism and peaks of species richness show a fairly high coincidence (compare Figs 6.4.b & d). In addition, single-cell endemics appear to show a fairly high coincidence, evidenced by the fact that only five out of the Guineo-Congolian near-minimum set of 17 are

irreplaceable (Rel. Irrep. = 0.29, Table 6.2.). This results in a near-minimum set that represents many species in relatively few grid cells, i.e. is very efficient (Rel. Set Size – Tot. Rich = 0.044; Table 6.2). In contrast, in the Northeastern Subregion, coincidence of peaks in species richness and narrow endemics is lower (compare the number of miss-matches in the north of the Ethiopian Highlands and Warsengalia Mountains in Figs 6.1.b & d). This means that irreplaceable grid cells selected to represent single-cell endemics will not necessarily also contain large numbers of more wide-spread species. Lack of co-occurrence of single-cell endemics is indicated by the fact that half of the near-minimum set consists of irreplaceable grid cells (Rel. Irrep. = 0.50, Table 6.2). Lack of co-occurrence of single-cell endemics and lack of coincidence of these single-cell endemics with peaks of species richness result in a large number of grid cells being required relative to the number of species the near-minimum set represents (Rel. Set Size – Tot. Rich. = 0.11, Table 6.2).

Lack of coincidence of narrow endemics in the Northeastern Subregion is probably partly due to the fact that both highland and lowland avifaunas contain narrow endemics. High levels of co-occurrence of narrow endemics and coincidence of narrow endemics with peaks of species richness in the Guineo-Congolian Subregion can possibly be explained by the location of centres of speciation in a few discrete forest refugia (Diamond & Hamilton 1980; Crowe & Crowe 1982; see Chapter 5 for more details). However, it must be noted that species richness in the Guineo-Congolian forests is highly correlated with general environmental stability and with amount and stability of productivity (Chapter 4). Consequently, it cannot be assumed that coincidence of species richness peaks with proposed refugia is causal; that is that elevated levels of speciation in refugia result in the high species richness levels observed in areas proposed to have been Pleistocene refugia. It is quite probable that refugia do occur in areas of high productivity and, particularly, stable environment (Fjeldså *et al.* 1997), such that the coincidence of species richness peaks with proposed refugia may be coincidental. Choice of either hypothesis is subjective, as they cannot be evaluated in a hypothetico-deductive framework (see also Tuomisto & Ruokailen 1997). The study of Fjeldså and co-workers (Fjeldså *et al.* 1997) also demonstrated that the effect of refugia in enhancing speciation rates need not be due only to climatic oscillations of the Pleistocene period. They suggested that climatic oscillations occurring in many epochs and over time

periods of varying length may also lead to speciation in refugia of local climatic stability (Fjeldså *et al.* 1997; see Chapters 4 & 5 for more discussion). Thus, the term refugium when used in this study indicates an area that has experienced a locally stable climate over many time periods, including, but not exclusively restricted to, the Pleistocene.

In the Southern Savanna Subregion, species richness and narrow endemism patterns are not nested. However, it would appear that grid cells selected to represent narrow endemics include a large portion of more widely distributed species. This may be, at least in part, due to the topographic range characteristic of many grid cells in this subregion. The narrow endemics of the Southern Savanna Subregion occur chiefly in the mountains, with more widespread species often occurring in lower lying areas. Thus, an apparent overlap of these species components in grid cells may not relate to actual sympatry of these species on the ground. This is a problem with 'flat' GIS grids, and also applies to apparent sympatry of species with stenotypic habitat requirements (e.g. Prendini 1995).

Species richness in the Southwestern Subregion is concentrated in the Karoo and an area of high species replacement between the western Kalahari and eastern Namib (Chapter 5; Williams *et al.* in press). Narrow endemism (both measures) is highly aggregated. No irreplaceable grid cells are identified in the near-minimum set (Fig 3g), indicating the relatively larger range-sizes of arid adapted species (e.g. Crowe & Brooke 1993; Little *et al.* 1996). Again some grid cells are selected because of apparent sympatry of species of lower (*Namibornis herero*) and higher altitudes (*Serinus leucolaema*) that probably does not exist 'on the ground'.

In the Horn of Africa Province of the Northern Arid Subregion, patterns of species richness and narrow endemism are similar (Fig. 6.6a – d), as most species of this subregion are the narrowly distributed. This results in six of the grid cells out of a near-minimum set of 12 being irreplaceable (Fig. 6.6f; Table 6.2). Levels of flexibility of priority cells selected in the Sahel are remarkably low, indicating low coincidence of species despite their apparently wide ranges. Their ranges are deceptively narrow. Despite apparently spanning a range of longitudes, actual numbers of grid cells inhabited are low.

The flexibility of the choice of a specific grid cell is determined by the narrowest range of the goal-essential species for which it was selected to represent. For example, the flexibility of the grid cell selected to represent the three bird species of the central Congo basin is determined by *Nectarinia congensis*, which occurs in only 19 grid cells, rather than *Afropavo congensis* (51 grid cells) and *Apalis goslingi* (100 grid cells). The greater flexibility of the Ituri grid cell (to the northeast of the Congo basin; Fig. 6.4f) is facilitated by the wider distribution of *Turdoides tenebrosus* (25 grid cells), being the most range-restricted of the species for which the Ituri grid cell was selected.

A biogeographical approach to complementarity analyses (that is the identification of a near-minimum set for each avifaunal subregion based on bird species strongly associated with that subregion) is less efficient than a sub-continental (subSaharan Africa) approach, requiring 4.8% more grid cells to represent all species once, and 9.7% to represent all species five times. However, a biogeographical approach helps to prevent the conservation of species in marginal areas. Selection of areas for conservation in biogeographical transition zones has been suggested to utilise the co-occurrence of many species in such habitats, which offer tantalisingly efficient solutions, catering for many species in few areas (Hockey & Branch 1994). However, the high species richness of transitional areas often coincides with the edges of species ranges (Winston & Angermeier 1995; Williams *et al.* in press) where species occur in marginal habitat at the extremes of their ecological tolerance (e.g. Gelderblom & Bronner 1995). Siting of conservation areas in such localities is probably not wise (Gelderblom *et al.* 1995; Gelderblom & Bronner 1995) especially as such areas are often dynamic in both composition and placement. A contrary opinion suggests that peripheral, marginal populations may have conservation value, representing valid components of within-species diversity (e.g. Winston & Angermeier 1995) and affording resilient buffers to population centre collapses (see Furow & Armijo-Prewitt 1995 for a synopsis). However, such studies are few and have no experimental basis, such that it might be a bit premature to hedge conservation on such suggestions.

Complementary areas in which grid cells that represent RD species are selected *a priori* need a total of 85 grid cells to represent the remaining 114 out of the 1230 subregion-associated species. This compares

favourably with the 79 grid cells required to represent all 1230 subregion-associated species in a sub-continental approach and the 89 grid cells required to represent these species at least once within their respective subregions. Consequently, the a priori selection of RD species does not incur a marked cost (in terms of near-minimum set size), and may prove a useful strategy to ensure that grid cells that represent RD species achieve high priority within a near-minimum set to represent Afrotropical birds.

CHAPTER 7. Synthesis

The goals of this thesis on the biogeography and conservation of terrestrial Afrotropical birds were threefold:

1. the description of patterns of distribution, including species richness, narrow endemism (as measured by indices of range-size rarity), and biogeographical zonation,
2. the investigation of possible causal roles of the current environment and history in the shaping of these patterns, and
3. the exploration of how aspects of distributional patterns may be used to prioritise local regions for conservation attention.

Analysis of presence data for terrestrial bird species restricted to the Afrotropics with distance indices and cluster analysis and the number of species unique to a cluster, led to the identification of a range of avifaunal zones. This approach did not neglect those avifaunas that are species poor (e.g. the Kalahari Province) or that have a small area extent (e.g. the Lake Turkana District). It also ensured representativeness in the resultant biogeographical classification scheme, which was not biased towards avifaunas that are species rich or that contain many narrow endemics, and further included avifaunas that consisted of few, but taxonomically and ecologically distinct species (e.g. the Namib Province). Analysis of zonal boundaries or areas exhibiting high levels of turnover, defined specifically as species replacement (as measured by neighbourhood segregation) were distinguished from zonal boundaries that are characterised by species richness gradients (as measured by neighbourhood heterogeneity). Analyses of these two separate components of zone boundary characteristics provided information on relative strength and breadth of boundaries between distinct avifaunas. For instance, the northern forest-savanna boundary between the Guineo-Congolian and Northern Savanna Subregions was shown to consist of a sharp ecotone between forest and savanna. A number of explorers have commented on how they walked north from full forest to completely open savanna in a matter of minutes (see Chapin 1932 for a discussion of comments made by early explorers and biologists). The northern forest-savanna is characterised by high species turnover, indicating the replacement of the forest avifauna by a distinct

savanna avifauna. This observation demonstrates that the avifauna of the Northern Savanna Subregion does not merely consist of a depauperate subset of the Guineo-Congolian avifauna, but rather that the Northern Savanna Subregion constitutes a unique avifauna that differs from that of the Guineo-Congolian Subregion. This is in contrast to the border between the Northern Savanna Subregion and Northern Arid Province of the Northern Arid Subregion, which is dominated by species drop-outs (or a decreasing species richness gradient as one moves from the Northern Savanna Subregion to the Northern Arid Province of the Northern Arid Subregion). This observation demonstrates that, in terms of terrestrial species endemic to subSaharan Africa, the Northern Arid Province of the Northern Arid Subregion represents a depauperate subset of the Northern Savanna Subregion. Findings of Williams *et al.* (in press) based on all terrestrial bird species occurring in subSaharan Africa show that the situation does not change with the inclusion of nonendemics and Palaearctic migrants. This finding emphasises the importance of environmental stability (both inter- and intra-annual) in determining species richness and concentrations of narrow endemics. As the Northern Arid Province of the Northern Arid Subregion experiences the greatest fluctuations in temperature and rainfall, and among the lowest levels of productivity and topography, which are also significant determinants of species richness, it is not surprising that the Northern Arid Province of the Northern Arid Subregion is species poor. This lack of stability, productivity and the uniform topography of the Northern Arid Province of the Northern Arid Subregion seem to have provided few to no opportunities for the formation of unique species. Species richness values for the Northern Arid Province of the Northern Arid Subregion are not boosted by Palaearctic migrants (cf. species replacement and richness gradient results in Williams *et al.* in press) despite its proximity to Europe, as most migrants over-fly the Northern Arid Province of the Northern Arid Subregion to reach the Northern Savanna Subregion, which has high productivity levels at the time of the migrants' arrival (Leisler 1992).

Analysis of zone boundary characteristics showed that the southern forest-savanna boundary between the Guineo-Congolian and Southern Savanna Subregions forms a gradient of replacement that takes place over a wide area extent. As with the turnover results for the northern forest-savanna transition, this

observation for the southern forest-savanna transition is verified by field observation (Chapin 1923, 1932, Lynes 1938). This transition is discussed in detail in Chapter 5.

The answer to the question of what the relative roles of the current environment and historical events (such as historical climatic oscillations, and formation of mountains, rivers and lakes) have been in shaping distributional patterns of birds in subSaharan Africa, and how these may affect conservation importance of avifaunal regions, is complex. Likely as not, these questions will never be resolved absolutely. These questions cannot be examined through the setting up and statistical testing of hypotheses (the scientific hypothetico-deductive method). As Cracraft and Prum (1988) and Tuomisto and Ruokolainen (1997) point out, testing of historical hypotheses is confounded by a paucity of relevant data and subjective interpretation of palaeoecological data, such that formulation and acceptance of historical hypotheses cannot be proven within hypothetico-deductive testing frameworks. Historical hypotheses are often derived from current patterns of distribution (e.g. Fjeldså *et al.* submitted). If one then calls on historical hypotheses generated in this manner to explain current patterns, one runs the risk of circularity entering into one's argument (Beven *et al.* 1984; Cracraft & Prum 1988). In addition, the effects of current environmental factors on species distribution can mask the effects of historical events (e.g. Roy *et al.* 1997). For example, modern redistribution of species distributions may obscure the locality and cause of the relevant speciation event (Beven *et al.* 1984; see Fjeldså *et al.* submitted for a discussion of these problems with respect to African bulbul and galago species). Moreover, current distributions may be coincidental with, rather than being due to, proposed dispersal or vicariance barriers. For instance, superspecies pairs that meet at rivers may not have originated from vicariance of the parental species by the river. The parental population may have been split by a contraction of suitable habitat. The superspecies members which resulted from the isolation may have expanded with improved conditions to meet at the river because it represents a dispersal barrier that neither member is able to cross. Alternatively, the contact line may be maintained coincidentally at the river (Louette 1992; Roy *et al.* 1997) by ecological differences on either side of the river (Tuomisto & Ruokolainen 1997) or by competition (see Cracraft & Prum 1988:615 for discussion of this idea). Lastly, current environmental factors that result in high species richness or concentrations of narrow endemics may coincide spatially

(geographically) with historical factors likely to have promoted species richness and narrow endemism (Fjeldså 1993; Fjeldså & Lovett 1997; Fjeldså *et al.* 1997; Tuomisto & Ruokolainen 1997). For instance, stability (or reliability) of current environmental factors, whether it be rainfall, temperature or productivity, is strongly and significantly correlated with both high species richness and concentrations of narrow endemics (Chapter 4). It is quite likely that current inter-annual stability is linked to localised areas that were climatically stable over longer term cycles (see Fjeldså *et al.* 1997 and references therein; Fjeldså *et al* submitted.). This has also been suggested for plants, which often show elevated levels of species richness and narrow endemism on mountains on the 'lee' to the Sahara desert, the shear size of which is suggested to have had a profound influence on local climatic regimes (H.P. Linder pers. comm.). Additionally, areas highlighted as currently experiencing stable climates often coincide with proposed Pleistocene refugia (e.g. Diamond & Hamilton 1980, Crowe & Crowe 1982; see Chapter 4 for further discussion). Both ideas express the importance of stability, the difference between the concepts being the length of the time cycle over which the influence of climatic instability affected patterns of speciation (neo-endemics) and persistence (relicts). The refugium hypothesis refers specifically to the climatic turbulence of the Pleistocene (Haffer 1969), while the 'localised stability' hypothesis suggests that, in addition to Pleistocene instability, climatic fluctuations over much shorter time scales may have driven speciation (Fjeldså & Lovett 1997, Fjeldså *et al.* 1997).

Clearly inter-annual stability is of the utmost importance. Interestingly, Jon Fjeldså and co-workers (Fjeldså 1994, Fjeldså & Rahbek in press) point to a probable coincidence of local areas of climatic stability and both ancient and modern cultures (see Fjeldså *et al.* in prep. for detailed listing of cultures that coincide with locally stable areas for both subSaharan Africa and the Neotropics). This points to how crucial it is that man interacts in a responsible and far-sighted manner with his environment. If lack of alternatives or greed destroy locally stable areas, people destroy the very resources that sustain them. For instance, removal of montane forest in Tanzania has been reported to coincide with the cessation of rainfall in the immediate area (J. Fjeldså pers. comm.). Montane forests can act to 'comb' moisture out of wind driven mist, resulting in local orographic rainfall (Fjeldså 1994, Fjeldså *et al.* in prep.). If such areas, characterised by locally mediated stable climates, are where future speciation will occur, then their

protection from destruction is vital. This is particularly so with the threat of global warming and climate change. Such locally stable climates may be crucial to organisms trying to find climatically suited refugia, as habitats and vegetation types migrate as dictated to climatic conditions.

Areas showing local climatic stability may not only be important to conservation because of their ability to protect species over the long term and due to their probable roles as centres of speciation. Such areas may also be important to conservation, because, in a number of subregions, they contain nested biotas. For instance, in the Guineo-Congolian Subregion, proposed refugia not only show co-occurrence of narrow endemics, but also show coincidence of peaks of species richness with peaks of narrow endemics. This facilitates efficient placement of priority areas in conservation planning. Co-occurrence of narrow endemics implies that few irreplaceable grid cells (that is grid cells selected to represent narrow endemics) are needed in a near minimum set determined by complementarity analysis to represent all species in a given data set. This reduces both the number of grid cells needed to represent all species (i.e. Set Size), and the number of irreplaceable grid cells in the near minimum set, and thus increases the flexibility of the set. This allows the complementarity algorithm greater freedom in the siting of grid cells in order to increase efficiency (measured here as the number of grid cells needed to represent all species). Coincidence of peaks in species richness with peaks of narrow endemism means that inflexible choices of grid cells selected to represent narrow endemics also contain many wider ranging species, representing high total numbers of species. This reduces the Set Size, and thus increases efficiency. The Northeastern Subregion represents an avifauna with low levels of nestedness. As a consequence, a relatively large number of grid cells are needed to represent few species (see Chapter 6 for details). Low levels of nestedness in the Northeastern avifauna may well be due to the lack of larger highland-lowland refugium complexes. Stability in the Northeastern Subregion is more likely to have been localised in small localities scattered throughout the Ethiopian Highlands and associated foothills (which have complex topography and may provide local amelioration of climatic conditions).

Results of this thesis demonstrate a complex interplay between current and historical environmental stability with patterns of distribution of Afrotropical birds. This interaction affects choice and efficiency

of techniques used to develop priorities for the selection of areas in which to focus conservation attention aimed at Afrotropical bird species.

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APPENDIX 2.1. List of the 1646 terrestrial birds species occurring regularly in subSaharan Africa. Life history categories: BB = species that breed in subSaharan Africa, BP = Palearctic migrants to the Afrotropics that have local breeding populations within the Afrotropics, PM = Palaearctic migrants, and MM = migrants from Madagascar. Distributional categories: ES = globally restricted to the Afrotropical region, ER = distribution centred in Afrotropical region but extending out of the Afrotropics, and NE = distribution centred outside the Afrotropics but extending into the Afrotropics (see Chapter 2 for details). Order of listing follows taxonomy presented in Sibley and Monroe (1990).

Species name			*Species name*		
Struthio camelus	BB	ES	*Francolinus castaneicollis*	BB	ES
Numida meleagris	BB	ER	*Francolinus nobilis*	BB	ES
Acryllium vulturinum	BB	ES	*Francolinus jacksoni*	BB	ES
Guttera plumifera	BB	ES	*Francolinus leucoscepus*	BB	ES
Guttera pucherani	BB	ES	*Francolinus rufopictus*	BB	ES
Agelastes meleagrides	BB	ES	*Francolinus afer*	BB	ES
Agelastes niger	BB	ES	*Francolinus swainsonii*	BB	ES
Francolinus lathami	BB	ES	*Coturnix coturnix*	BP	NE
Francolinus coqui	BB	ES	*Coturnix delegorguei*	BB	ER
Francolinus albogularis	BB	ES	*Coturnix adansonii*	BB	ES
Francolinus schlegelii	BB	ES	*Ptilopachus petrosus*	BB	ES
Francolinus streptophorus	BB	ES	*Afropavo congensis*	BB	ES
Francolinus finschi	BB	ES	*Xenoperdix udzungwensis*	BB	ES
Francolinus africanus	BB	ES	*Turnix sylvatica*	BB	NE
Francolinus levaillantii	BB	ES	*Turnix nana*	BB	ES
Francolinus levaillantoides	BB	ES	*Turnix hottentotta*	BB	ES
Francolinus psilolaemus	BB	ES	*Ortyxelos meiffrenii*	BB	ES
Francolinus shelleyi	BB	ES	*Gymnobucco calvus*	BB	ES
Francolinus sephaena	BB	ES	*Gymnobucco peli*	BB	ES
Francolinus ahantensis	BB	ES	*Gymnobucco sladeni*	BB	ES
Francolinus squamatus	BB	ES	*Gymnobucco bonapartei*	BB	ES
Francolinus griseostriatus	BB	ES	*Stactolaema leucotis*	BB	ES
Francolinus nahani	BB	ES	*Stactolaema anchietae*	BB	ES
Francolinus hartlaubi	BB	ES	*Stactolaema whytii*	BB	ES
Francolinus hildebrandti	BB	ES	*Stactolaema olivacea*	BB	ES
Francolinus natalensis	BB	ES	*Pogoniulus scolopaceus*	BB	ES
Francolinus bicalcaratus	BB	ER	*Pogoniulus coryphaeus*	BB	ES
Francolinus clappertoni	BB	ES	*Pogoniulus leucomystax*	BB	ES
Francolinus icterorhynchus	BB	ES	*Pogoniulus simplex*	BB	ES
Francolinus harwoodi	BB	ES	*Pogoniulus atroflavus*	BB	ES
Francolinus capensis	BB	ES	*Pogoniulus subsulphureus*	BB	ES
Francolinus adspersus	BB	ES	*Pogoniulus bilineatus*	BB	ES
Francolinus camerunensis	BB	ES	*Pogoniulus chrysoconus*	BB	ES
Francolinus swierstrai	BB	ES	*Pogoniulus pusillus*	BB	ES
Francolinus erckelii	BB	ES	*Buccanodon duchaillui*	BB	ES
Francolinus ochropectus	BB	ES	*Tricholaema hirsuta*	BB	ES

Species name			*Species name*		
Tricholaema diademata	BB	ES	*Campethera tullbergi*	BB	ES
Tricholaema frontata	BB	ES	*Campethera nivosa*	BB	ES
Tricholaema leucomelas	BB	ES	*Campethera caroli*	BB	ES
Tricholaema lachrymosa	BB	ES	*Geocolaptes olivaceus*	BB	ES
Tricholaema melanocephala	BB	ES	*Dendropicos elachus*	BB	ES
Lybius undatus	BB	ES	*Dendropicos poecilolaemus*	BB	ES
Lybius vieilloti	BB	ES	*Dendropicos abyssinicus*	BB	ES
Lybius leucocephalus	BB	ES	*Dendropicos fuscescens*	BB	ES
Lybius chaplini	BB	ES	*Dendropicos lugubris*	BB	ES
Lybius rubrifacies	BB	ES	*Dendropicos gabonensis*	BB	ES
Lybius guifsobalito	BB	ES	*Dendropicos stierlingi*	BB	ES
Lybius torquatus	BB	ES	*Dendropicos namaquus*	BB	ES
Lybius melanopterus	BB	ES	*Dendropicos pyrrhogaster*	BB	ES
Lybius minor	BB	ES	*Dendropicos xantholophus*	BB	ES
Lybius bidentatus	BB	ES	*Dendropicos elliotii*	BB	ES
Lybius dubius	BB	ES	*Dendropicos goertae*	BB	ES
Lybius rolleti	BB	ES	*Dendropicos spodocephalus*	BB	ES
Trachyphonus purpuratus	BB	ES	*Dendropicos griseocephalus*	BB	ES
Trachyphonus vaillantii	BB	ES	*Dendropicos obsoletus*	BB	ES
Trachyphonus margaritatus	BB	ES	*Upupa epops*	PM	NE
Trachyphonus erythrocephalus	BB	ES	*Upupa africana*	BB	ES
Trachyphonus darnaudii	BB	ES	*Phoeniculus purpureus*	BB	ES
Trachyphonus usambiro	BB	ES	*Phoeniculus damarensis*	BB	ES
Indicator maculatus	BB	ES	*Phoeniculus somaliensis*	BB	ES
Indicator variegatus	BB	ES	*Phoeniculus bollei*	BB	ES
Indicator indicator	BB	ES	*Phoeniculus castaneiceps*	BB	ES
Indicator minor	BB	ES	*Rhinopomastus aterrimus*	BB	ES
Indicator conirostris	BB	ES	*Rhinopomastus cyanomelas*	BB	ES
Indicator willcocksi	BB	ES	*Rhinopomastus minor*	BB	ES
Indicator exilis	BB	ES	*Bucorvus abyssinicus*	BB	ES
Indicator pumilio	BB	ES	*Bucorvus leadbeateri*	BB	ES
Indicator meliphilus	BB	ES	*Tockus albocristatus*	BB	ES
Melichneutes robustus	BB	ES	*Tockus hartlaubi*	BB	ES
Melignomon eisentrauti	BB	ES	*Tockus camurus*	BB	ES
Melignomon zenkeri	BB	ES	*Tockus monteiri*	BB	ES
Prodotiscus insignis	BB	ES	*Tockus erythrorhynchus*	BB	ES
Prodotiscus zambesiae	BB	ES	*Tockus flavirostris*	BB	ES
Prodotiscus regulus	BB	ES	*Tockus leucomelas*	BB	ES
Jynx torquilla	PM	NE	*Tockus jacksonii*	BB	ES
Jynx ruficollis	BB	ES	*Tockus deckeni*	BB	ES
Sasia africana	BB	ES	*Tockus alboterminatus*	BB	ES
Campethera punctuligera	BB	ES	*Tockus bradfieldi*	BB	ES
Campethera nubica	BB	ES	*Tockus fasciatus*	BB	ES
Campethera bennettii	BB	ES	*Tockus hemprichii*	BB	ES
Campethera scriptoricauda	BB	ES	*Tockus nasutus*	BB	ES
Campethera abingoni	BB	ES	*Tockus pallidirostris*	BB	ES
Campethera mombassica	BB	ES	*Ceratogymna bucinator*	BB	ES
Campethera notata	BB	ES	*Ceratogymna fistulator*	BB	ES
Campethera maculosa	BB	ES	*Ceratogymna brevis*	BB	ES
Campethera cailliautii	BB	ES	*Ceratogymna subcylindricus*	BB	ES

Species name			*Species name*		
Ceratogymna cylindrius	BB	ES	*Centropus neumanni*	BB	ES
Ceratogymna albotibialis	BB	ES	*Centropus monachus*	BB	ES
Ceratogymna atrata	BB	ES	*Centropus senegalensis*	BB	ER
Ceratogymna elata	BB	ES	*Centropus superciliosus*	BB	ER
Apaloderma narina	BB	ES	*Centropus burchelli*	BB	ES
Apaloderma aequatoriale	BB	ES	*Oxylophus jacobinus*	BB	NE
Apaloderma vittatum	BB	ES	*Oxylophus levaillantii*	BB	ES
Coracias garrulus	PM	NE	*Clamator glandarius*	BP	NE
Coracias abyssinica	BB	ER	*Pachycoccyx audeberti*	BB	ER
Coracias caudata	BB	ES	*Cuculus solitarius*	BB	ES
Coracias spatulata	BB	ES	*Cuculus clamosus*	BB	ES
Coracias naevia	BB	ES	*Cuculus canorus*	PM	NE
Coracias cyanogaster	BB	ES	*Cuculus gularis*	BB	ES
Eurystomus glaucurus	BB	ER	*Cuculus poliocephalus*	PM	NE
Eurystomus gularis	BB	ER	*Cuculus rochii*	MM	ER
Merops gularis	BB	ES	*Cercococcyx mechowi*	BB	ES
Merops muelleri	BB	ES	*Cercococcyx olivinus*	BB	ES
Merops bulocki	BB	ES	*Cercococcyx montanus*	BB	ES
Merops bullockoides	BB	ES	*Chrysococcyx flavigularis*	BB	ES
Merops pusillus	BB	ES	*Chrysococcyx klaas*	BB	ES
Merops variegatus	BB	ES	*Chrysococcyx cupreus*	BB	ES
Merops oreobates	BB	ES	*Chrysococcyx caprius*	BB	NE
Merops hirundineus	BB	ES	*Ceuthmochares aereus*	BB	ES
Merops breweri	BB	ES	*Psittacus erithacus*	BB	ES
Merops revoilii	BB	ES	*Poicephalus robustus*	BB	ES
Merops albicollis	BB	ER	*Poicephalus gulielmi*	BB	ES
Merops orientalis	BB	NE	*Poicephalus senegalus*	BB	ES
Merops boehmi	BB	ES	*Poicephalus crassus*	BB	ES
Merops persicus	PM	NE	*Poicephalus meyeri*	BB	ES
Merops superciliosus	BB	ER	*Poicephalus flavifrons*	BB	ES
Merops apiaster	BP	NE	*Poicephalus rufiventris*	BB	ES
Merops malimbicus	BB	ES	*Poicephalus cryptoxanthus*	BB	ES
Merops nubicus	BB	ES	*Poicephalus rueppellii*	BB	ES
Merops nubicoides	BB	ES	*Agapornis pullarius*	BB	ES
Ispidina picta	BB	ES	*Agapornis taranta*	BB	ES
Ispidina lecontei	BB	ES	*Agapornis swindernianus*	BB	ES
Halcyon badia	BB	ES	*Agapornis roseicollis*	BB	ES
Halcyon leucocephala	BB	NE	*Agapornis fischeri*	BB	ES
Halcyon senegalensis	BB	ES	*Agapornis personatus*	BB	ES
Halcyon malimbica	BB	ES	*Agapornis lilianae*	BB	ES
Halcyon albiventris	BB	ES	*Agapornis nigrigenis*	BB	ES
Halcyon chelicuti	BB	ES	*Psittacula krameri*	BB	NE
Colius striatus	BB	ES	*Schoutedenapus myioptilus*	BB	ES
Colius leucocephalus	BB	ES	*Schoutedenapus schoutedeni*	BB	ES
Colius castanotus	BB	ES	*Telacanthura ussheri*	BB	ES
Colius colius	BB	ES	*Telacanthura melanopygia*	BB	ES
Urocolius macrourus	BB	ES	*Rhaphidura sabini*	BB	ES
Urocolius indicus	BB	ES	*Neafrapus cassini*	BB	ES
Centropus leucogaster	BB	ES	*Neafrapus boehmi*	BB	ES
Centropus anselli	BB	ES	*Cypsiurus parvus*	BB	ER

Species name			*Species name*		
Tachymarptis melba	BP	NE	*Glaucidium perlatum*	BB	ES
Tachymarptis aequatorialis	BB	ES	*Glaucidium tephronotum*	BB	ES
Apus apus	PM	NE	*Glaucidium sjostedti*	BB	ES
Apus niansae	BB	ES	*Glaucidium capense*	BB	ES
Apus pallidus	PM	NE	*Glaucidium castaneum*	BB	ES
Apus barbatus	BB	ES	*Glaucidium ngamiense*	BB	ES
Apus berliozi	BB	ES	*Glaucidium scheffleri*	BB	ES
Apus bradfieldi	BB	ES	*Glaucidium albertinum*	BB	ES
Apus affinis	BB	NE	*Athene noctua*	BB	NE
Apus horus	BB	ES	*Asio otus*	BB	NE
Apus toulsoni	BB	ES	*Asio abyssinicus*	BB	ES
Apus caffer	BB	NE	*Asio flammeus*	PM	NE
Apus batesi	BB	ES	*Asio capensis*	BB	ER
Tauraco persa	BB	ES	*Tyto alba*	BB	NE
Tauraco schuetti	BB	ES	*Tyto capensis*	BB	ES
Tauraco schalowi	BB	ES	*Phodilus prigoginei*	BB	ES
Tauraco fischeri	BB	ES	*Caprimulgus binotatus*	BB	ES
Tauraco livingstonii	BB	ES	*Caprimulgus europaeus*	PM	NE
Tauraco corythaix	BB	ES	*Caprimulgus fraenatus*	BB	ES
Tauraco bannermani	BB	ES	*Caprimulgus rufigena*	BB	ES
Tauraco erythrolophus	BB	ES	*Caprimulgus aegyptius*	PM	NE
Tauraco macrorhynchus	BB	ES	*Caprimulgus nubicus*	BB	NE
Tauraco leucotis	BB	ES	*Caprimulgus eximius*	BB	ES
Tauraco ruspolii	BB	ES	*Caprimulgus donaldsoni*	BB	ES
Tauraco hartlaubi	BB	ES	*Caprimulgus nigriscapularis*	BB	ES
Tauraco leucolophus	BB	ES	*Caprimulgus pectoralis*	BB	ES
Musophaga johnstoni	BB	ES	*Caprimulgus prigoginei*	BB	ES
Musophaga porphyreolopha	BB	ES	*Caprimulgus poliocephalus*	BB	ES
Musophaga violacea	BB	ES	*Caprimulgus ruwenzorii*	BB	ES
Musophaga rossae	BB	ES	*Caprimulgus natalensis*	BB	ES
Corythaixoides concolor	BB	ES	*Caprimulgus inornatus*	BB	ER
Corythaixoides personatus	BB	ES	*Caprimulgus stellatus*	BB	ES
Corythaixoides leucogaster	BB	ES	*Caprimulgus tristigma*	BB	ES
Crinifer piscator	BB	ES	*Caprimulgus batesi*	BB	ES
Crinifer zonurus	BB	ES	*Caprimulgus climacurus*	BB	ES
Corythaeola cristata	BB	ES	*Caprimulgus clarus*	BB	ES
Otus icterorhynchus	BB	ES	*Caprimulgus fossii*	BB	ES
Otus ireneae	BB	ES	*Caprimulgus solala*	BB	ES
Otus scops	BP	NE	*Macrodipteryx longipennis*	BB	ES
Otus leucotis	BB	ES	*Macrodipteryx vexillaria*	BB	ES
Bubo ascalaphus	BB	NE	*Columba livia*	BB	NE
Bubo capensis	BB	ES	*Columba guinea*	BB	ES
Bubo africanus	BB	ER	*Columba albitorques*	BB	ES
Bubo poensis	BB	ES	*Columba oliviae*	BB	ES
Bubo vosserleri	BB	ES	*Columba unicincta*	BB	ES
Bubo shelleyi	BB	ES	*Columba sjostedti*	BB	ES
Bubo lacteus	BB	ES	*Columba arquatrix*	BB	ES
Bubo leucostictus	BB	ES	*Columba albinucha*	BB	ES
Strix woodfordii	BB	ES	*Columba iriditorques*	BB	ES
Jubula lettii	BB	ES	*Columba delegorguei*	BB	ES

Species name			*Species name*		
Columba larvata	BB	ES	*Vanellus tectus*	BB	ES
Streptopelia turtur	PM	NE	*Vanellus melanocephalus*	BB	ES
Streptopelia hypopyrrha	BB	ES	*Vanellus lugubris*	BB	ES
Streptopelia lugens	BB	ES	*Vanellus melanopterus*	BB	ES
Streptopelia senegalensis	BB	NE	*Vanellus coronatus*	BB	ES
Streptopelia decipiens	BB	ES	*Vanellus superciliosus*	BB	ES
Streptopelia vinacea	BB	ES	*Burhinus capensis*	BB	ER
Streptopelia capicola	BB	ES	*Rhinoptilus africanus*	BB	ES
Streptopelia semitorquata	BB	ER	*Rhinoptilus chalcopterus*	BB	ES
Streptopelia roseogrisea	BB	ER	*Rhinoptilus cinctus*	BB	ES
Streptopelia reichenowi	BB	ES	*Cursorius cursor*	BB	NE
Turtur abyssinicus	BB	ES	*Cursorius rufus*	BB	ES
Turtur chalcospilos	BB	ES	*Cursorius temminckii*	BB	ES
Turtur afer	BB	ES	*Polihierax semitorquatus*	BB	ES
Turtur tympanistria	BB	ES	*Falco naumanni*	PM	NE
Turtur brehmeri	BB	ES	*Falco tinnunculus*	PM	NE
Oena capensis	BB	ER	*Falco rupicoloides*	BB	ES
Treron waalia	BB	ER	*Falco dlopex*	BB	ES
Treron calva	BB	ES	*Falco ardosiaceus*	BB	ES
Sarothrura elegans	BB	ES	*Falco dickinsoni*	BB	ES
Sarothrura affinis	BB	ES	*Falco chicquera*	BB	NE
Neotis denhami	BB	ES	*Falco vespertinus*	PM	NE
Neotis ludwigi	BB	ES	*Falco amurensis*	PM	NE
Neotis nuba	BB	ES	*Falco eleonorae*	PM	NE
Neotis heuglinii	BB	ES	*Falco concolor*	PM	NE
Ardeotis arabs	BB	ER	*Falco subbuteo*	PM	NE
Ardeotis kori	BB	ES	*Falco cuvierii*	BB	ES
Eupodotis savilei	BB	ES	*Falco biarmicus*	BB	NE
Eupodotis gindiana	BB	ES	*Falco cherrug*	PM	NE
Eupodotis ruficrista	BB	ES	*Falco peregrinus*	BP	NE
Eupodotis afraoides	BB	ES	*Falco pelegrinoides*	BB	NE
Eupodotis afra	BB	ES	*Falco fasciinucha*	BB	ES
Eupodotis rueppellii	BB	ES	*Sagittarius serpentarius*	BB	ES
Eupodotis vigorsii	BB	ES	*Aviceda cuculoides*	BB	ES
Eupodotis humilis	BB	ES	*Pernis apivorus*	PM	NE
Eupodotis senegalensis	BB	ES	*Macheiramphus alcinus*	BB	NE
Eupodotis caerulescens	BB	ES	*Elanus caeruleus*	BB	NE
Eupodotis melanogaster	BB	ES	*Chelictinia riocourii*	BB	ES
Eupodotis hartlaubii	BB	ES	*Milvus migrans*	BP	NE
Grus paradisea	BB	ES	*Gypohierax angolensis*	BB	ES
Pterocles namaqua	BB	ES	*Gypaetus barbatus*	BB	NE
Pterocles exustus	BB	NE	*Neophron percnopterus*	BP	NE
Pterocles senegallus	BB	NE	*Necrosyrtes monachus*	BB	ES
Pterocles gutturalis	BB	ES	*Gyps africanus*	BB	ES
Pterocles decoratus	BB	ES	*Gyps rueppellii*	BB	ER
Pterocles bicinctus	BB	ES	*Gyps fulvus*	PM	NE
Pterocles quadricinctus	BB	ES	*Gyps coprotheres*	BB	ES
Pterocles lichtensteinii	BB	NE	*Torgos tracheliotus*	BB	NE
Pterocles burchelli	BB	ES	*Trigonoceps occipitalis*	BB	ES
Gallinago media	PM	NE	*Circaetus gallicus*	BP	NE

Species name			*Species name*		
Circaetus pectoralis	BB	ES	*Ciconia abdimii*	BB	ER
Circaetus cinereus	BB	ES	*Ciconia ciconia*	BP	NE
Circaetus fasciolatus	BB	ES	*Leptoptilos crumeniferus*	BB	ES
Circaetus cinerascens	BB	ES	*Smithornis capensis*	BB	ES
Terathopius ecaudatus	BB	ER	*Smithornis sharpei*	BB	ES
Dryotriorchis spectabilis	BB	ES	*Smithornis rufolateralis*	BB	ES
Circus maurus	BB	ES	*Pseudocalyptomena graueri*	BB	ES
Circus macrourus	PM	NE	*Pitta angolensis*	BB	ES
Polyboroides typus	BB	ES	*Pitta reichenowi*	BB	ES
Kaupifalco monogrammicus	BB	ES	*Lanius collurio*	PM	NE
Melierax metabates	BB	ER	*Lanius isabellinus*	PM	NE
Melierax poliopterus	BB	ES	*Lanius gubernator*	BB	ES
Melierax canorus	BB	ES	*Lanius souzae*	BB	ES
Micronisus gabar	BB	ER	*Lanius minor*	PM	NE
Accipiter toussenelii	BB	ES	*Lanius excubitor*	PM	NE
Accipiter tachiro	BB	ES	*Lanius excubitoroides*	BB	ES
Accipiter castanilius	BB	ES	*Lanius cabanisi*	BB	ES
Accipiter badius	BB	NE	*Lanius dorsalis*	BB	ES
Accipiter brevipes	PM	NE	*Lanius somalicus*	BB	ES
Accipiter erythropus	BB	ES	*Lanius mackinnoni*	BB	ES
Accipiter minullus	BB	ES	*Lanius collaris*	BB	ES
Accipiter ovampensis	BB	ES	*Lanius marwitzi*	BB	ES
Accipiter nisus	PM	NE	*Lanius senator*	PM	NE
Accipiter rufiventris	BB	ES	*Lanius nubicus*	PM	NE
Accipiter melanoleucus	BB	ES	*Corvinella corvina*	BB	ES
Urotriorchis macrourus	BB	ES	*Corvinella melanoleuca*	BB	ES
Butastur rufipennis	BB	ES	*Eurocephalus rueppelli*	BB	ES
Buteo buteo	PM	NE	*Eurocephalus anguitimens*	BB	ES
Buteo oreophilus	BB	ES	*Zavattariornis stresemanni*	BB	ES
Buteo rufinus	PM	NE	*Pyrrhocorax pyrrhocorax*	BB	NE
Buteo auguralis	BB	ES	*Ptilostomus afer*	BB	ES
Buteo augur	BB	ES	*Corvus capensis*	BB	ES
Buteo archeri	BB	ES	*Corvus albus*	BB	ER
Buteo rufofuscus	BB	ES	*Corvus ruficollis*	BB	NE
Aquila pomarina	PM	NE	*Corvus rhipidurus*	BB	NE
Aquila clanga	PM	NE	*Corvus albicollis*	BB	ES
Aquila rapax	BP	NE	*Corvus crassirostris*	BB	ES
Aquila heliaca	PM	NE	*Oriolus oriolus*	PM	NE
Aquila wahlbergi	BB	ES	*Oriolus auratus*	BB	ES
Aquila verreauxi	BB	NE	*Oriolus chlorocephalus*	BB	ES
Hieraaetus spilogaster	BB	ES	*Oriolus brachyrhynchus*	BB	ES
Hieraaetus pennatus	PM	NE	*Oriolus monacha*	BB	ES
Hieraaetus ayresii	BB	ES	*Oriolus larvatus*	BB	ES
Polemaetus bellicosus	BB	ES	*Oriolus percivali*	BB	ES
Lophaetus occipitalis	BB	ES	*Oriolus nigripennis*	BB	ES
Spizaetus africanus	BB	ES	*Coracina pectoralis*	BB	ES
Stephanoaetus coronatus	BB	ES	*Coracina caesia*	BB	ES
Bostrychia carunculata	BB	ES	*Coracina azurea*	BB	ES
Geronticus eremita	PM	NE	*Coracina graueri*	BB	ES
Geronticus calvus	BB	ES	*Campephaga petiti*	BB	ES

Species name			*Species name*		
Campephaga flava	BB	ES	*Laniarius leucorhynchus*	BB	ES
Campephaga phoenicea	BB	ES	*Laniarius poensis*	BB	ES
Campephaga quiscalina	BB	ES	*Laniarius fuelleborni*	BB	ES
Campephaga lobata	BB	ES	*Rhodophoneus cruentus*	BB	ES
Campephaga oriolina	BB	ES	*Telophorus zeylonus*	BB	ES
Dicrurus ludwigii	BB	ES	*Telophorus bocagei*	BB	ES
Dicrurus atripennis	BB	ES	*Telophorus sulfureopectus*	BB	ES
Dicrurus adsimilis	BB	ES	*Telophorus olivaceus*	BB	ES
Dicrurus modestus	BB	ES	*Telophorus multicolor*	BB	ES
Erythrocercus livingstonei	BB	ES	*Telophorus nigrifrons*	BB	ES
Erythrocercus mccallii	BB	ES	*Telophorus kupeensis*	BB	ES
Erythrocercus holochlorus	BB	ES	*Telophorus viridis*	BB	ES
Elminia longicauda	BB	ES	*Telophorus dohertyi*	BB	ES
Elminia albicauda	BB	ES	*Telophorus quadricolor*	BB	ES
Trochocercus nigromitratus	BB	ES	*Malaconotus cruentus*	BB	ES
Trochocercus albiventris	BB	ES	*Malaconotus lagdeni*	BB	ES
Trochocercus albonotatus	BB	ES	*Malaconotus gladiator*	BB	ES
Trochocercus nitens	BB	ES	*Malaconotus blanchoti*	BB	ES
Trochocercus cyanomelas	BB	ES	*Malaconotus monteiri*	BB	ES
Terpsiphone rufiventer	BB	ES	*Malaconotus alius*	BB	ES
Terpsiphone bedfordi	BB	ES	*Prionops plumatus*	BB	ES
Terpsiphone rufocinerea	BB	ES	*Prionops poliolophus*	BB	ES
Terpsiphone viridis	BB	ES	*Prionops alberti*	BB	ES
Lanioturdus torquatus	BB	ES	*Prionops caniceps*	BB	ES
Nilaus afer	BB	ES	*Prionops rufiventris*	BB	ES
Dryoscopus gambensis	BB	ES	*Prionops retzii*	BB	ES
Dryoscopus pringlii	BB	ES	*Prionops gabela*	BB	ES
Dryoscopus cubla	BB	ES	*Prionops scopifrons*	BB	ES
Dryoscopus senegalensis	BB	ES	*Bias flammulatus*	BB	ES
Dryoscopus angolensis	BB	ES	*Bias musicus*	BB	ES
Dryoscopus sabini	BB	ES	*Batis diops*	BB	ES
Tchagra minuta	BB	ES	*Batis margaritae*	BB	ES
Tchagra anchietae	BB	ES	*Batis mixta*	BB	ES
Tchagra senegala	BB	ER	*Batis reichenowi*	BB	ES
Tchagra australis	BB	ES	*Batis dimorpha*	BB	ES
Tchagra jamesi	BB	ES	*Batis capensis*	BB	ES
Tchagra tchagra	BB	ES	*Batis fratrum*	BB	ES
Laniarius ruficeps	BB	ES	*Batis molitor*	BB	ES
Laniarius luehderi	BB	ES	*Batis soror*	BB	ES
Laniarius brauni	BB	ES	*Batis pririt*	BB	ES
Laniarius amboimensis	BB	ES	*Batis senegalensis*	BB	ES
Laniarius liberatus	BB	ES	*Batis orientalis*	BB	ES
Laniarius turatii	BB	ES	*Batis minor*	BB	ES
Laniarius aethiopicus	BB	ES	*Batis perkeo*	BB	ES
Laniarius ferrugineus	BB	ES	*Batis minima*	BB	ES
Laniarius barbarus	BB	ES	*Batis ituriensis*	BB	ES
Laniarius erythrogaster	BB	ES	*Batis occulta*	BB	ES
Laniarius atrococcineus	BB	ES	*Batis minulla*	BB	ES
Laniarius atroflavus	BB	ES	*Platysteira cyanea*	BB	ES
Laniarius funebris	BB	ES	*Platysteira laticincta*	BB	ES

Species name			*Species name*		
Platysteira albifrons	BB	ES	*Bradornis microrhynchus*	BB	ES
Platysteira peltata	BB	ES	*Dioptrornis brunneus*	BB	ES
Platysteira castanea	BB	ES	*Dioptrornis chocolatinus*	BB	ES
Platysteira tonsa	BB	ES	*Dioptrornis fischeri*	BB	ES
Platysteira blissetti	BB	ES	*Melaenornis annamarulae*	BB	ES
Platysteira chalybea	BB	ES	*Melaenornis ardesiacus*	BB	ES
Platysteira jamesoni	BB	ES	*Melaenornis edolioides*	BB	ES
Platysteira concreta	BB	ES	*Melaenornis pammelaina*	BB	ES
Chaetops frenatus	BB	ES	*Fraseria ocreata*	BB	ES
Chaetops aurantius	BB	ES	*Fraseria cinerascens*	BB	ES
Picathartes gymnocephalus	BB	ES	*Sigelus silens*	BB	ES
Picathartes oreas	BB	ES	*Muscicapa striata*	PM	NE
Neocossyphus finschii	BB	ES	*Muscicapa gambagae*	BB	ER
Neocossyphus fraseri	BB	ES	*Muscicapa ussheri*	BB	ES
Neocossyphus rufus	BB	ES	*Muscicapa infuscata*	BB	ES
Neocossyphus poensis	BB	ES	*Muscicapa boehmi*	BB	ES
Monticola rupestris	BB	ES	*Muscicapa aquatica*	BB	ES
Monticola explorator	BB	ES	*Muscicapa olivascens*	BB	ES
Monticola brevipes	BB	ES	*Muscicapa lendu*	BB	ES
Monticola pretoriae	BB	ES	*Muscicapa itombwensis*	BB	ES
Monticola angolensis	BB	ES	*Muscicapa adusta*	BB	ES
Monticola saxatilis	PM	NE	*Muscicapa epulata*	BB	ES
Monticola rufocinereus	BB	ER	*Muscicapa sethsmithi*	BB	ES
Monticola solitarius	PM	NE	*Muscicapa comitata*	BB	ES
Zoothera piaggiae	BB	ES	*Muscicapa tessmanni*	BB	ES
Zoothera tanganjicae	BB	ES	*Muscicapa caerulescens*	BB	ES
Zoothera crossleyi	BB	ES	*Myioparus griseigularis*	BB	ES
Zoothera gurneyi	BB	ES	*Myioparus plumbeus*	BB	ES
Zoothera oberlaenderi	BB	ES	*Ficedula hypoleuca*	PM	NE
Zoothera cameronensis	BB	ES	*Ficedula albicollis*	PM	NE
Zoothera princei	BB	ES	*Ficedula semitorquata*	PM	NE
Zoothera kibalensis	BB	ES	*Pogonocichla stellata*	BB	ES
Zoothera guttata	BB	ES	*Swynnertonia swynnertoni*	BB	ES
Psophocichla litsipsirupa	BB	ES	*Stiphrornis erythrothorax*	BB	ES
Turdus pelios	BB	ES	*Sheppardia poensis*	BB	ES
Turdus tephronotus	BB	ES	*Sheppardia bocagei*	BB	ES
Turdus libonyanus	BB	ES	*Sheppardia cyornithopsis*	BB	ES
Turdus olivaceus	BB	ES	*Sheppardia aequatorialis*	BB	ES
Turdus smithii	BB	ES	*Sheppardia sharpei*	BB	ES
Alethe poliocephala	BB	ES	*Sheppardia gunningi*	BB	ES
Alethe poliophrys	BB	ES	*Sheppardia gabela*	BB	ES
Alethe fuelleborni	BB	ES	*Sheppardia montana*	BB	ES
Alethe choloensis	BB	ES	*Sheppardia lowei*	BB	ES
Alethe diademata	BB	ES	*Luscinia luscinia*	PM	NE
Alethe castanea	BB	ES	*Luscinia megarhynchos*	PM	NE
Empidornis semipartitus	BB	ES	*Luscinia svecica*	PM	NE
Bradornis pallidus	BB	ES	*Irania gutturalis*	PM	NE
Bradornis infuscatus	BB	ES	*Cossypha isabellae*	BB	ES
Bradornis mariquensis	BB	ES	*Cossypha roberti*	BB	ES
Bradornis pumilus	BB	ES	*Cossypha archeri*	BB	ES

Species name			*Species name*		
Cossypha anomala	BB	ES	*Cercomela dubia*	BB	ES
Cossypha caffra	BB	ES	*Cercomela melanura*	BB	NE
Cossypha humeralis	BB	ES	*Cercomela sordida*	BB	ES
Cossypha cyanocampter	BB	ES	*Myrmecocichla aethiops*	BB	ES
Cossypha polioptera	BB	ES	*Myrmecocichla albifrons*	BB	ES
Cossypha semirufa	BB	ES	*Myrmecocichla arnotti*	BB	ES
Cossypha heuglini	BB	ES	*Myrmecocichla formicivora*	BB	ES
Cossypha natalensis	BB	ES	*Myrmecocichla melaena*	BB	ES
Cossypha dichroa	BB	ES	*Myrmecocichla nigra*	BB	ES
Cossypha heinrichi	BB	ES	*Myrmecocichla tholloni*	BB	ES
Cossypha niveicapilla	BB	ES	*Thamnolaea cinnamomeiventris*	BB	ES
Cossypha albicapilla	BB	ES	*Thamnolaea coronata*	BB	ES
Xenocopsychus ansorgei	BB	ES	*Thamnolaea semirufa*	BB	ES
Cichladusa arquata	BB	ES	*Pinarornis plumosus*	BB	ES
Cichladusa ruficauda	BB	ES	*Poeoptera stuhlmanni*	BB	ES
Cichladusa guttata	BB	ES	*Poeoptera kenricki*	BB	ES
Cercotrichas leucosticta	BB	ES	*Poeoptera lugubris*	BB	ES
Cercotrichas quadrivirgata	BB	ES	*Grafisia torquata*	BB	ES
Cercotrichas barbata	BB	ES	*Onychognathus walleri*	BB	ES
Cercotrichas signata	BB	ES	*Onychognathus nabouroup*	BB	ES
Cercotrichas hartlaubi	BB	ES	*Onychognathus morio*	BB	ES
Cercotrichas leucophrys	BB	ES	*Onychognathus blythii*	BB	ES
Cercotrichas galactotes	BP	NE	*Onychognathus fulgidus*	BB	ES
Cercotrichas paena	BB	ES	*Onychognathus tenuirostris*	BB	ES
Cercotrichas coryphaeus	BB	ES	*Onychognathus albirostris*	BB	ES
Cercotrichas podobe	BB	ER	*Onychognathus salvadorii*	BB	ES
Namibornis herero	BB	ES	*Coccycolius iris*	BB	ES
Phoenicurus ochruros	PM	NE	*Lamprotornis cupreocauda*	BB	ES
Phoenicurus phoenicurus	PM	NE	*Lamprotornis purpureiceps*	BB	ES
Saxicola rubetra	PM	NE	*Lamprotornis corruscus*	BB	ES
Saxicola torquata	BP	NE	*Lamprotornis purpureus*	BB	ES
Saxicola bifasciata	BB	ES	*Lamprotornis nitens*	BB	ES
Oenanthe leucopyga	BB	NE	*Lamprotornis chalcurus*	BB	ES
Oenanthe monticola	BB	ES	*Lamprotornis chalybaeus*	BB	ES
Oenanthe phillipsi	BB	ES	*Lamprotornis chloropterus*	BB	ES
Oenanthe oenanthe	PM	NE	*Lamprotornis elisabeth*	BB	ES
Oenanthe lugubris	BB	ES	*Lamprotornis acuticaudus*	BB	ES
Oenanthe pleschanka	PM	NE	*Lamprotornis australis*	BB	ES
Oenanthe hispanica	PM	NE	*Lamprotornis splendidus*	BB	ES
Oenanthe xanthoprymna	PM	NE	*Lamprotornis mevesii*	BB	ES
Oenanthe deserti	PM	NE	*Lamprotornis caudatus*	BB	ES
Oenanthe pileata	BB	ES	*Lamprotornis purpuropterus*	BB	ES
Oenanthe isabellina	PM	NE	*Lamprotornis superbus*	BB	ES
Oenanthe bottae	BB	ER	*Lamprotornis pulcher*	BB	ES
Oenanthe heuglini	BB	ES	*Lamprotornis shelleyi*	BB	ES
Cercomela sinuata	BB	ES	*Lamprotornis hildebrandti*	BB	ES
Cercomela schlegelii	BB	ES	*Cinnyricinclus sharpii*	BB	ES
Cercomela tractrac	BB	ES	*Cinnyricinclus femoralis*	BB	ES
Cercomela familiaris	BB	ES	*Cinnyricinclus leucogaster*	BB	ER
Cercomela scotocerca	BB	ES	*Speculipastor bicolor*	BB	ES

Species name			*Species name*		
Neocichla gutturalis	BB	ES	*Hirundo preussi*	BB	ES
Spreo fischeri	BB	ES	*Hirundo rufigula*	BB	ES
Spreo bicolor	BB	ES	*Hirundo spilodera*	BB	ES
Spreo albicapillus	BB	ES	*Hirundo fuliginosa*	BB	ES
Cosmopsarus regius	BB	ES	*Delichon urbica*	PM	NE
Cosmopsarus unicolor	BB	ES	*Psalidoprocne nitens*	BB	ES
Creatophora cinerea	BB	ES	*Psalidoprocne fuliginosa*	BB	ES
Buphagus africanus	BB	ES	*Psalidoprocne albiceps*	BB	ES
Buphagus erythrorhynchus	BB	ES	*Psalidoprocne chalybea*	BB	ES
Salpornis spilonotus	BB	NE	*Psalidoprocne petiti*	BB	ES
Anthoscopus punctifrons	BB	ES	*Psalidoprocne mangbettorum*	BB	ES
Anthoscopus parvulus	BB	ES	*Psalidoprocne oleaginea*	BB	ES
Anthoscopus musculus	BB	ES	*Psalidoprocne pristoptera*	BB	ES
Anthoscopus flavifrons	BB	ES	*Psalidoprocne antinorii*	BB	ES
Anthoscopus caroli	BB	ES	*Psalidoprocne orientalis*	BB	ES
Anthoscopus sylviella	BB	ES	*Psalidoprocne holomelas*	BB	ES
Anthoscopus minutus	BB	ES	*Psalidoprocne obscura*	BB	ES
Pholidornis rushiae	BB	ES	*Pycnonotus barbatus*	BB	ER
Parus guineensis	BB	ES	*Pycnonotus somaliensis*	BB	ES
Parus leucomelas	BB	ES	*Pycnonotus dodsoni*	BB	ES
Parus niger	BB	ES	*Pycnonotus tricolor*	BB	ES
Parus albiventris	BB	ES	*Pycnonotus nigricans*	BB	ES
Parus leuconotus	BB	ES	*Pycnonotus capensis*	BB	ES
Parus funereus	BB	ES	*Andropadus montanus*	BB	ES
Parus rufiventris	BB	ES	*Andropadus kakamegae*	BB	ES
Parus fringillinus	BB	ES	*Andropadus masukuensis*	BB	ES
Parus pallidiventris	BB	ES	*Andropadus virens*	BB	ES
Parus fasciiventer	BB	ES	*Andropadus gracilis*	BB	ES
Parus thruppi	BB	ES	*Andropadus ansorgei*	BB	ES
Parus griseiventris	BB	ES	*Andropadus curvirostris*	BB	ES
Parus cinerascens	BB	ES	*Andropadus gracilirostris*	BB	ES
Parus afer	BB	ES	*Andropadus importunus*	BB	ES
Hirundo griseopyga	BB	ES	*Andropadus latirostris*	BB	ES
Hirundo rupestris	PM	NE	*Andropadus tephrolaemus*	BB	ES
Hirundo obsoleta	BB	NE	*Andropadus nigriceps*	BB	ES
Hirundo fuligula	BB	ES	*Andropadus chlorigula*	BB	ES
Hirundo lucida	BB	ES	*Andropadus olivaceiceps*	BB	ES
Hirundo aethiopica	BB	ES	*Andropadus milanjensis*	BB	ES
Hirundo angolensis	BB	ES	*Calyptocichla serina*	BB	ES
Hirundo albigularis	BB	ES	*Baeopogon indicator*	BB	ES
Hirundo nigrorufa	BB	ES	*Baeopogon clamans*	BB	ES
Hirundo atrocaerulea	BB	ES	*Ixonotus guttatus*	BB	ES
Hirundo leucosoma	BB	ES	*Chlorocichla simplex*	BB	ES
Hirundo megaensis	BB	ES	*Chlorocichla flavicollis*	BB	ES
Hirundo dimidiata	BB	ES	*Chlorocichla falkensteini*	BB	ES
Hirundo cucullata	BB	ES	*Chlorocichla flaviventris*	BB	ES
Hirundo semirufa	BB	ES	*Chlorocichla laetissima*	BB	ES
Hirundo senegalensis	BB	ES	*Chlorocichla prigoginei*	BB	ES
Hirundo daurica	BP	NE	*Thescelocichla leucopleura*	BB	ES
Hirundo domicella	BB	ES	*Phyllastrephus scandens*	BB	ES

Species name			*Species name*		
Phyllastrephus cabanisi	BB	ES	*Cisticola subruficapillus*	BB	ES
Phyllastrephus fischeri	BB	ES	*Cisticola lais*	BB	ES
Phyllastrephus placidus	BB	ES	*Cisticola distinctus*	BB	ES
Phyllastrephus terrestris	BB	ES	*Cisticola restrictus*	BB	ES
Phyllastrephus strepitans	BB	ES	*Cisticola njombe*	BB	ES
Phyllastrephus fulviventris	BB	ES	*Cisticola angolensis*	BB	ES
Phyllastrephus cerviniventris	BB	ES	*Cisticola robustus*	BB	ES
Phyllastrephus baumanni	BB	ES	*Cisticola aberdare*	BB	ES
Phyllastrephus hypochloris	BB	ES	*Cisticola natalensis*	BB	ES
Phyllastrephus poensis	BB	ES	*Cisticola fulvicapillus*	BB	ES
Phyllastrephus lorenzi	BB	ES	*Cisticola angusticauda*	BB	ES
Phyllastrephus poliocephalus	BB	ES	*Cisticola melanurus*	BB	ES
Phyllastrephus flavostriatus	BB	ES	*Cisticola brachypterus*	BB	ES
Phyllastrephus alfredi	BB	ES	*Cisticola rufus*	BB	ES
Phyllastrephus debilis	BB	ES	*Cisticola troglodytes*	BB	ES
Phyllastrephus albigularis	BB	ES	*Cisticola nanus*	BB	ES
Phyllastrephus icterinus	BB	ES	*Cisticola juncidis*	BB	NE
Phyllastrephus leucolepis	BB	ES	*Cisticola aridulus*	BB	ES
Phyllastrephus xavieri	BB	ES	*Cisticola textrix*	BB	ES
Bleda syndactyla	BB	ES	*Cisticola eximius*	BB	ES
Bleda eximia	BB	ES	*Cisticola dambo*	BB	ES
Bleda canicapilla	BB	ES	*Cisticola brunnescens*	BB	ES
Nicator chloris	BB	ES	*Cisticola ayresii*	BB	ES
Nicator gularis	BB	ES	*Prinia gracilis*	BB	NE
Nicator vireo	BB	ES	*Prinia subflava*	BB	ES
Criniger barbatus	BB	ES	*Prinia somalica*	BB	ES
Criniger calurus	BB	ES	*Prinia fluviatilis*	BB	ES
Criniger chloronotus	BB	ES	*Prinia flavicans*	BB	ES
Criniger ndussumensis	BB	ES	*Prinia maculosa*	BB	ES
Criniger olivaceus	BB	ES	*Prinia leontica*	BB	ES
Neolestes torquatus	BB	ES	*Prinia leucopogon*	BB	ES
Cisticola erythrops	BB	ES	*Prinia bairdii*	BB	ES
Cisticola lepe	BB	ES	*Prinia melanops*	BB	ES
Cisticola cantans	BB	ES	*Phragmacia substriata*	BB	ES
Cisticola lateralis	BB	ES	*Oreophilais robertsi*	BB	ES
Cisticola anonymus	BB	ES	*Heliolais erythroptera*	BB	ES
Cisticola woosnami	BB	ES	*Malcorus pectoralis*	BB	ES
Cisticola bulliens	BB	ES	*Drymocichla incana*	BB	ES
Cisticola discolor	BB	ES	*Urolais epichlora*	BB	ES
Cisticola chubbi	BB	ES	*Spiloptila clamans*	BB	ES
Cisticola hunteri	BB	ES	*Apalis pulchra*	BB	ES
Cisticola emini	BB	ES	*Apalis ruwenzorii*	BB	ES
Cisticola nigriloris	BB	ES	*Apalis thoracica*	BB	ES
Cisticola aberrans	BB	ES	*Apalis nigriceps*	BB	ES
Cisticola bodessa	BB	ES	*Apalis jacksoni*	BB	ES
Cisticola chinianus	BB	ES	*Apalis chariessa*	BB	ES
Cisticola cinereolus	BB	ES	*Apalis binotata*	BB	ES
Cisticola ruficeps	BB	ES	*Apalis personata*	BB	ES
Cisticola mongalla	BB	ES	*Apalis flavida*	BB	ES
Cisticola rufilatus	BB	ES	*Apalis viridiceps*	BB	ES

Species name			*Species name*		
Apalis ruddi	BB	ES	*Hippolais languida*	PM	NE
Apalis sharpei	BB	ES	*Hippolais olivetorum*	PM	NE
Apalis rufogularis	BB	ES	*Hippolais polyglotta*	PM	NE
Apalis argentea	BB	ES	*Hippolais icterina*	PM	NE
Apalis bamendae	BB	ES	*Chloropeta natalensis*	BB	ES
Apalis goslingi	BB	ES	*Chloropeta similis*	BB	ES
Apalis porphyrolaema	BB	ES	*Stenostira scita*	BB	ES
Apalis kaboboensis	BB	ES	*Phyllolais pulchella*	BB	ES
Apalis chapini	BB	ES	*Orthotomus metopias*	BB	ES
Apalis melanocephala	BB	ES	*Orthotomus moreaui*	BB	ES
Apalis chirindensis	BB	ES	*Poliolais lopezi*	BB	ES
Apalis cinerea	BB	ES	*Graueria vittata*	BB	ES
Apalis alticola	BB	ES	*Eremomela icteropygialis*	BB	ES
Apalis karamojae	BB	ES	*Eremomela salvadorii*	BB	ES
Apalis rufifrons	BB	ES	*Eremomela flavocrissalis*	BB	ES
Hypergerus atriceps	BB	ES	*Eremomela pusilla*	BB	ES
Eminia lepida	BB	ES	*Eremomela canescens*	BB	ES
Camaroptera brevicaudata	BB	ES	*Eremomela gregalis*	BB	ES
Camaroptera harterti	BB	ES	*Eremomela scotops*	BB	ES
Camaroptera brachyura	BB	ES	*Eremomela badiceps*	BB	ES
Camaroptera superciliaris	BB	ES	*Eremomela turneri*	BB	ES
Camaroptera chloronota	BB	ES	*Eremomela atricollis*	BB	ES
Calamonastes simplex	BB	ES	*Eremomela usticollis*	BB	ES
Calamonastes stierlingi	BB	ES	*Sylvietta virens*	BB	ES
Calamonastes fasciolatus	BB	ES	*Sylvietta denti*	BB	ES
Euryptila subcinnamomea	BB	ES	*Sylvietta chapini*	BB	ES
Speirops melanocephalus	BB	ES	*Sylvietta leucophrys*	BB	ES
Zosterops senegalensis	BB	ES	*Sylvietta brachyura*	BB	ES
Zosterops poliogaster	BB	ES	*Sylvietta philippae*	BB	ES
Zosterops abyssinicus	BB	ER	*Sylvietta ruficapilla*	BB	ES
Zosterops pallidus	BB	ES	*Sylvietta whytii*	BB	ES
Bradypterus grandis	BB	ES	*Sylvietta isabellina*	BB	ES
Bradypterus alfredi	BB	ES	*Sylvietta rufescens*	BB	ES
Bradypterus sylvaticus	BB	ES	*Hemitesia neumanni*	BB	ES
Bradypterus lopezi	BB	ES	*Macrosphenus kempi*	BB	ES
Bradypterus mariae	BB	ES	*Macrosphenus flavicans*	BB	ES
Bradypterus barratti	BB	ES	*Macrosphenus concolor*	BB	ES
Bradypterus cinnamomeus	BB	ES	*Macrosphenus pulitzeri*	BB	ES
Bradypterus victorini	BB	ES	*Macrosphenus kretschmeri*	BB	ES
Bathmocercus cerviniventris	BB	ES	*Hylia prasina*	BB	ES
Bathmocercus rufus	BB	ES	*Phylloscopus laetus*	BB	ES
Scepomycter winifredae	BB	ES	*Phylloscopus laurae*	BB	ES
Melocichla mentalis	BB	ES	*Phylloscopus ruficapillus*	BB	ES
Achaetopus pycnopygius	BB	ES	*Phylloscopus herberti*	BB	ES
Sphenoaecus afer	BB	ES	*Phylloscopus budongoensis*	BB	ES
Locustella naevia	PM	NE	*Phylloscopus umbrovirens*	BB	ER
Locustella fluviatilis	PM	NE	*Phylloscopus trochilus*	PM	NE
Acrocephalus scripaceus	PM	NE	*Phylloscopus collybita*	PM	NE
Acrocephalus palustris	PM	NE	*Phylloscopus bonelli*	PM	NE
Hippolais pallida	BP	NE	*Phylloscopus sibilatrix*	PM	NE

Species name			*Species name*		
Hyliota flavigaster	BB	ES	*Sylvia hortensis*	PM	NE
Hyliota australis	BB	ES	*Sylvia leucomelaena*	BB	NE
Hyliota violacea	BB	ES	*Sylvia rueppelli*	PM	NE
Schoenicola brevirostris	BB	ES	*Sylvia melanocephala*	PM	NE
Modulatrix stictigula	BB	ES	*Sylvia cantillans*	PM	NE
Arcanator orostruthus	BB	ES	*Sylvia mystacea*	PM	NE
Illadopsis cleaveri	BB	ES	*Sylvia conspicillata*	PM	NE
Illadopsis albipectus	BB	ES	*Mirafra passerina*	BB	ES
Illadopsis rufescens	BB	ES	*Mirafra cantillans*	BB	NE
Illadopsis puveli	BB	ES	*Mirafra cheniana*	BB	ES
Illadopsis rufipennis	BB	ES	*Mirafra albicauda*	BB	ES
Illadopsis fulvescens	BB	ES	*Mirafra cordofanica*	BB	ES
Illadopsis pyrrhoptera	BB	ES	*Mirafra williamsi*	BB	ES
Illadopsis atriceps	BB	ES	*Mirafra pulpa*	BB	ES
Illadopsis abyssinica	BB	ES	*Mirafra hypermetra*	BB	ES
Kakamega poliothorax	BB	ES	*Mirafra somalica*	BB	ES
Ptyrticus turdinus	BB	ES	*Mirafra ashi*	BB	ES
Turdoides fulvus	BB	ER	*Mirafra africana*	BB	ES
Turdoides aylmeri	BB	ES	*Mirafra sharpii*	BB	ES
Turdoides rubiginosus	BB	ES	*Mirafra angolensis*	BB	ES
Turdoides reinwardtii	BB	ES	*Mirafra rufocinnamomea*	BB	ES
Turdoides tenebrosus	BB	ES	*Mirafra apiata*	BB	ES
Turdoides melanops	BB	ES	*Mirafra collaris*	BB	ES
Turdoides squamulatus	BB	ES	*Mirafra africanoides*	BB	ES
Turdoides leucopygius	BB	ES	*Mirafra alopex*	BB	ES
Turdoides hartlaubii	BB	ES	*Mirafra rufa*	BB	ES
Turdoides bicolor	BB	ES	*Mirafra gilletti*	BB	ES
Turdoides sharpei	BB	ES	*Mirafra poecilosterna*	BB	ES
Turdoides hypoleucus	BB	ES	*Mirafra degodiensis*	BB	ES
Turdoides hindei	BB	ES	*Mirafra naevia*	BB	ES
Turdoides leucocephalus	BB	ES	*Mirafra sabota*	BB	ES
Turdoides plebejus	BB	ES	*Pinarocorys erythropygia*	BB	ES
Turdoides jardineii	BB	ES	*Pinarocorys nigricans*	BB	ES
Turdoides gymnogenys	BB	ES	*Heteromirafra archeri*	BB	ES
Lioptilus nigricapillus	BB	ES	*Heteromirafra sidamoensis*	BB	ES
Kupeornis gilberti	BB	ES	*Heteromirafra ruddi*	BB	ES
Kupeornis rufocinctus	BB	ES	*Certhilauda curvirostris*	BB	ES
Kupeornis chapini	BB	ES	*Certhilauda chuana*	BB	ES
Parophasma galinieri	BB	ES	*Certhilauda erythrochlamys*	BB	ES
Phyllanthus atripennis	BB	ES	*Certhilauda albescens*	BB	ES
Sylvia lugens	BB	ES	*Certhilauda burra*	BB	ES
Sylvia boehmi	BB	ES	*Certhilauda barlowi*	BB	ES
Sylvia layardi	BB	ES	*Chersomanes albofasciata*	BB	ES
Sylvia subcaeruleum	BB	ES	*Eremopterix leucotis*	BB	ES
Sylvia atricapilla	PM	NE	*Eremopterix australis*	BB	ES
Sylvia borin	PM	NE	*Eremopterix verticalis*	BB	ES
Sylvia communis	PM	NE	*Eremopterix leucopareia*	BB	ES
Sylvia curruca	PM	NE	*Eremopterix signata*	BB	ES
Sylvia nana	PM	NE	*Eremopterix nigriceps*	BB	NE
Sylvia nisoria	PM	NE	*Ammomanes cincturus*	BB	NE

Species name			*Species name*		
Ammomanes deserti	BB	NE	*Nectarinia cyanolaema*	BB	ES
Ammomanes grayi	BB	ES	*Nectarinia fuliginosa*	BB	ES
Alaemon alaudipes	BB	NE	*Nectarinia amethystina*	BB	ES
Alaemon hamertoni	BB	ES	*Nectarinia rubescens*	BB	ES
Melanocorypha bimaculata	PM	NE	*Nectarinia senegalensis*	BB	ES
Calandrella brachydactyla	PM	NE	*Nectarinia hunteri*	BB	ES
Calandrella blanfordi	BB	ER	*Nectarinia adelberti*	BB	ES
Calandrella erlangeri	BB	ES	*Nectarinia venusta*	BB	ES
Calandrella cinerea	BB	ES	*Nectarinia ursulae*	BB	ES
Calandrella somalica	BB	ES	*Nectarinia talatala*	BB	ES
Calandrella athensis	BB	ES	*Nectarinia oustaleti*	BB	ES
Spizocorys conirostris	BB	ES	*Nectarinia bouvieri*	BB	ES
Spizocorys sclateri	BB	ES	*Nectarinia osea*	BB	NE
Spizocorys obbiensis	BB	ES	*Nectarinia habessinica*	BB	ER
Spizocorys personata	BB	ES	*Nectarinia manoensis*	BB	ES
Spizocorys fringillaris	BB	ES	*Nectarinia chalybea*	BB	ES
Eremalauda starki	BB	ES	*Nectarinia ludovicensis*	BB	ES
Eremalauda dunni	BB	ER	*Nectarínia prigoginei*	BB	ES
Galerida cristata	BB	NE	*Nectarinia stuhlmanni*	BB	ES
Galerida theklae	BB	NE	*Nectarinia preussi*	BB	ES
Galerida modesta	BB	ES	*Nectarinia afra*	BB	ES
Galerida magnirostris	BB	ES	*Nectarinia mediocris*	BB	ES
Pseudalaemon fremantlii	BB	ES	*Nectarinia neergaardi*	BB	ES
Promerops gurneyi	BB	ES	*Nectarinia chloropygia*	BB	ES
Promerops cafer	BB	ES	*Nectarinia minulla*	BB	ES
Anthreptes fraseri	BB	ES	*Nectarinia regia*	BB	ES
Anthreptes axillaris	BB	ES	*Nectarinia loveridgei*	BB	ES
Anthreptes reichenowi	BB	ES	*Nectarinia moreaui*	BB	ES
Anthreptes anchietae	BB	ES	*Nectarinia rockefelleri*	BB	ES
Anthreptes gabonicus	BB	ES	*Nectarinia cuprea*	BB	ES
Anthreptes longuemarei	BB	ES	*Nectarinia fusca*	BB	ES
Anthreptes orientalis	BB	ES	*Nectarinia rufipennis*	BB	ES
Anthreptes neglectus	BB	ES	*Nectarinia tacazze*	BB	ES
Anthreptes aurantium	BB	ES	*Nectarinia purpureiventris*	BB	ES
Anthreptes pallidigaster	BB	ES	*Nectarinia bocagii*	BB	ES
Anthreptes rectirostris	BB	ES	*Nectarinia kilimensis*	BB	ES
Anthreptes rubritorques	BB	ES	*Nectarinia reichenowi*	BB	ES
Anthreptes collaris	BB	ES	*Nectarinia famosa*	BB	ES
Anthreptes platurus	BB	ES	*Nectarinia johnstoni*	BB	ES
Anthreptes metallicus	BB	ER	*Nectarinia shelleyi*	BB	ES
Nectarinia seimundi	BB	ES	*Nectarinia erythrocerca*	BB	ES
Nectarinia batesi	BB	ES	*Nectarinia congensis*	BB	ES
Nectarinia olivacea	BB	ES	*Nectarinia mariquensis*	BB	ES
Nectarinia violacea	BB	ES	*Nectarinia bifasciata*	BB	ES
Nectarinia veroxii	BB	ES	*Nectarinia pembae*	BB	ES
Nectarinia reichenbachii	BB	ES	*Nectarinia coccinigastra*	BB	ES
Nectarinia oritis	BB	ES	*Nectarinia johannae*	BB	ES
Nectarinia alinae	BB	ES	*Nectarinia superba*	BB	ES
Nectarinia verticalis	BB	ES	*Nectarinia pulchella*	BB	ES
Nectarinia bannermani	BB	ES	*Nectarinia nectarinioides*	BB	ES

Species name			*Species name*		
Passer castanopterus	BB	ES	*Sporopipes squamifrons*	BB	ES
Passer rufocinctus	BB	ES	*Plocepasser mahali*	BB	ES
Passer motitensis	BB	ES	*Plocepasser superciliosus*	BB	ES
Passer melanurus	BB	ES	*Plocepasser rufoscapulatus*	BB	ES
Passer griseus	BB	ES	*Plocepasser donaldsoni*	BB	ES
Passer swainsonii	BB	ES	*Histurgops ruficauda*	BB	ES
Passer gongonensis	BB	ES	*Pseudonigrita arnaudi*	BB	ES
Passer suahelicus	BB	ES	*Pseudonigrita cabanisi*	BB	ES
Passer diffusus	BB	ES	*Philetairus socius*	BB	ES
Passer simplex	BB	NE	*Ploceus bannermani*	BB	ES
Passer luteus	BB	ER	*Ploceus batesi*	BB	ES
Passer euchlorus	BB	ER	*Ploceus nigrimentum*	BB	ES
Passer eminibey	BB	ES	*Ploceus baglafecht*	BB	ES
Petronia pyrgita	BB	ES	*Ploceus bertrandi*	BB	ES
Petronia superciliaris	BB	ES	*Ploceus pelzelni*	BB	ES
Petronia dentata	BB	ER	*Ploceus subpersonatus*	BB	ES
Carpospiza brachydactyla	PM	NE	*Ploceus luteolus*	BB	ES
Motacilla alba	PM	NE	*Ploceus intermedius*	BB	ES
Motacilla capensis	BB	ES	*Ploceus ocularis*	BB	ES
Motacilla flava	PM	NE	*Ploceus nigricollis*	BB	ES
Tmetothylacus tenellus	BB	ES	*Ploceus melanogaster*	BB	ES
Macronyx croceus	BB	ES	*Ploceus alienus*	BB	ES
Macronyx fuellebornii	BB	ES	*Ploceus temporalis*	BB	ES
Macronyx capensis	BB	ES	*Ploceus capensis*	BB	ES
Macronyx flavicollis	BB	ES	*Ploceus xanthops*	BB	ES
Macronyx aurantiigula	BB	ES	*Ploceus bojeri*	BB	ES
Anthus sharpei	BB	ES	*Ploceus castaneiceps*	BB	ES
Anthus chloris	BB	ES	*Ploceus galbula*	BB	ER
Anthus lineiventris	BB	ES	*Ploceus heuglini*	BB	ES
Anthus crenatus	BB	ES	*Ploceus victoriae*	BB	ES
Anthus cinnamomeus	BB	ER	*Ploceus vitellinus*	BB	ES
Anthus camaroonensis	BB	ES	*Ploceus velatus*	BB	ES
Anthus hoeschi	BB	ES	*Ploceus katangae*	BB	ES
Anthus leucophrys	BB	ES	*Ploceus ruweti*	BB	ES
Anthus vaalensis	BB	ES	*Ploceus reichardi*	BB	ES
Anthus pallidiventris	BB	ES	*Ploceus cucullatus*	BB	ES
Anthus melindae	BB	ES	*Ploceus spekei*	BB	ES
Anthus campestris	PM	NE	*Ploceus nigerrimus*	BB	ES
Anthus bannermani	BB	ES	*Ploceus weynsi*	BB	ES
Anthus latistriatus	BB	ES	*Ploceus golandi*	BB	ES
Anthus similis	BB	NE	*Ploceus jacksoni*	BB	ES
Anthus nyassae	BB	ES	*Ploceus badius*	BB	ES
Anthus brachyurus	BB	ES	*Ploceus rubiginosus*	BB	ES
Anthus caffer	BB	ES	*Ploceus aureonucha*	BB	ES
Anthus sokokensis	BB	ES	*Ploceus tricolor*	BB	ES
Anthus trivialis	PM	NE	*Ploceus albinucha*	BB	ES
Bubalornis albirostris	BB	ES	*Ploceus bicolor*	BB	ES
Bubalornis niger	BB	ES	*Ploceus preussi*	BB	ES
Dinemellia dinemelli	BB	ES	*Ploceus dorsomaculatus*	BB	ES
Sporopipes frontalis	BB	ES	*Ploceus nicolli*	BB	ES

Species name			*Species name*		
Ploceus olivaceiceps	BB	ES	*Cryptospiza shelleyi*	BB	ES
Ploceus insignis	BB	ES	*Pyrenestes sanguineus*	BB	ES
Ploceus angolensis	BB	ES	*Pyrenestes ostrinus*	BB	ES
Pachyphantes superciliosus	BB	ES	*Pyrenestes minor*	BB	ES
Malimbus flavipes	BB	ES	*Spermophaga poliogenys*	BB	ES
Malimbus coronatus	BB	ES	*Spermophaga haematina*	BB	ES
Malimbus cassini	BB	ES	*Spermophaga ruficapilla*	BB	ES
Malimbus ballmanni	BB	ES	*Clytospiza monteiri*	BB	ES
Malimbus racheliae	BB	ES	*Hypargos niveoguttatus*	BB	ES
Malimbus scutatus	BB	ES	*Hypargos margaritatus*	BB	ES
Malimbus ibadanensis	BB	ES	*Euschistospiza dybowskii*	BB	ES
Malimbus erythrogaster	BB	ES	*Euschistospiza cinereovinacea*	BB	ES
Malimbus malimbicus	BB	ES	*Lagonosticta rufopicta*	BB	ES
Malimbus rubricollis	BB	ES	*Lagonosticta nitidula*	BB	ES
Anaplectes rubriceps	BB	ES	*Lagonosticta senegala*	BB	ES
Brachycope anomala	BB	ES	*Lagonosticta rara*	BB	ES
Quelea cardinalis	BB	ES	*Lagonosticta rubricata*	BB	ES
Quelea quelea	BB	ES	*Lagonosticta landanae*	BB	ES
Euplectes afer	BB	ES	*Lagonosticta virata*	BB	ES
Euplectes diadematus	BB	ES	*Lagonosticta umbrinodorsalis*	BB	ES
Euplectes gierowii	BB	ES	*Lagonosticta rhodopareia*	BB	ES
Euplectes hordeaceus	BB	ES	*Lagonosticta vinacea*	BB	ES
Euplectes orix	BB	ES	*Lagonosticta larvata*	BB	ES
Euplectes nigroventris	BB	ES	*Uraeginthus angolensis*	BB	ES
Euplectes aureus	BB	ES	*Uraeginthus bengalus*	BB	ES
Euplectes capensis	BB	ES	*Uraeginthus cyanocephalus*	BB	ES
Euplectes axillaris	BB	ES	*Uraeginthus ianthinogaster*	BB	ES
Euplectes albonotatus	BB	ES	*Uraeginthus granatina*	BB	ES
Euplectes ardens	BB	ES	*Estrilda caerulescens*	BB	ES
Euplectes psammocromius	BB	ES	*Estrilda perreini*	BB	ES
Euplectes progne	BB	ES	*Estrilda thomensis*	BB	ES
Euplectes jacksoni	BB	ES	*Estrilda quartinia*	BB	ES
Anomalospiza imberbis	BB	ES	*Estrilda melanotis*	BB	ES
Parmoptila rubrifrons	BB	ES	*Estrilda poliopareia*	BB	ES
Parmoptila woodhousei	BB	ES	*Estrilda paludicola*	BB	ES
Nigrita fusconota	BB	ES	*Estrilda ochrogaster*	BB	ES
Nigrita bicolor	BB	ES	*Estrilda melpoda*	BB	ES
Nigrita luteifrons	BB	ES	*Estrilda rhodopyga*	BB	ES
Nigrita canicapilla	BB	ES	*Estrilda troglodytes*	BB	ES
Nesocharis shelleyi	BB	ES	*Estrilda astrild*	BB	ES
Nesocharis capistrata	BB	ES	*Estrilda nigriloris*	BB	ES
Pytilia phoenicoptera	BB	ES	*Estrilda nonnula*	BB	ES
Pytilia lineata	BB	ES	*Estrilda atricapilla*	BB	ES
Pytilia afra	BB	ES	*Estrilda kandti*	BB	ES
Pytilia melba	BB	ES	*Estrilda charmosyna*	BB	ES
Pytilia hypogrammica	BB	ES	*Estrilda erythronotus*	BB	ES
Mandingoa nitidula	BB	ES	*Ortygospiza atricollis*	BB	ES
Cryptospiza reichenovii	BB	ES	*Ortygospiza gabonensis*	BB	ES
Cryptospiza salvadorii	BB	ES	*Ortygospiza locustella*	BB	ES
Cryptospiza jacksoni	BB	ES	*Lonchura cantans*	BB	NE

Species name			*Species name*		
Lonchura griseicapilla	BB	ES	*Serinus mozambicus*	BB	ES
Lonchura cucullata	BB	ES	*Serinus donaldsoni*	BB	ES
Lonchura bicolor	BB	ES	*Serinus buchanani*	BB	ES
Lonchura nigriceps	BB	ES	*Serinus dorsostriatus*	BB	ES
Lonchura fringilloides	BB	ES	*Serinus flaviventris*	BB	ES
Amadina fasciata	BB	ES	*Serinus sulphuratus*	BB	ES
Amadina erythrocephala	BB	ES	*Serinus albogularis*	BB	ES
Vidua chalybeata	BB	ES	*Serinus canicapillus*	BB	ES
Vidua raricola	BB	ES	*Serinus reichardi*	BB	ES
Vidua larvaticola	BB	ES	*Serinus gularis*	BB	ES
Vidua funerea	BB	ES	*Serinus mennelli*	BB	ES
Vidua codringtoni	BB	ES	*Serinus tristriatus*	BB	ES
Vidua purpurascens	BB	ES	*Serinus ankoberensis*	BB	ES
Vidua wilsoni	BB	ES	*Serinus striolatus*	BB	ES
Vidua hypocherina	BB	ES	*Serinus whytii*	BB	ES
Vidua fischeri	BB	ES	*Serinus burtoni*	BB	ES
Vidua regia	BB	ES	*Serinus melanochrous*	BB	ES
Vidua macroura	BB	ES	*Serinus leucopterus*	BB	ES
Vidua orientalis	BB	ES	*Serinus totta*	BB	ES
Vidua togoensis	BB	ES	*Serinus symonsi*	BB	ES
Vidua interjecta	BB	ES	*Serinus leucolaema*	BB	ES
Vidua paradisea	BB	ES	*Serinus alario*	BB	ES
Vidua obtusa	BB	ES	*Linurgus olivaceus*	BB	ES
Serinus canicollis	BB	ES	*Rhynchostruthus socotranus*	BB	ER
Serinus nigriceps	BB	ES	*Carduelis johannis*	BB	ES
Serinus frontalis	BB	ES	*Rhodopechys githaginea*	PM	NE
Serinus citrinelloides	BB	ES	*Emberiza cineracea*	PM	NE
Serinus hypostictus	BB	ES	*Emberiza hortulana*	PM	NE
Serinus capistratus	BB	ES	*Emberiza caesia*	PM	NE
Serinus koliensis	BB	ES	*Emberiza striolata*	BB	NE
Serinus scotops	BB	ES	*Emberiza impetuani*	BB	ES
Serinus leucopygius	BB	ES	*Emberiza tahapisi*	BB	ER
Serinus flavigula	BB	ES	*Emberiza capensis*	BB	ES
Serinus xanthopygius	BB	ES	*Emberiza flaviventris*	BB	ES
Serinus reichenowi	BB	ES	*Emberiza poliopleura*	BB	ES
Serinus atrogularis	BB	ES	*Emberiza affinis*	BB	ES
Serinus citrinipectus	BB	ES	*Emberiza cabanisi*	BB	ES

APPENDIX 2.2. References used to compile distributional information for 1646 terrestrial bird species occurring on the mainland of subSaharan Africa.

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APPENDIX 2.3. Species defined as waterbirds according to the definition outlined in Chapter 2. Order of listing follows taxonomy presented in Sibley and Monroe (1990).

Dendrocygna bicolor
Dendrocygna viduata
Thalassornis leuconotus
Oxyura maccoa
Cyanochen cyanopterus
Alopochen aegyptiacus
Tadorna ferruginea
Tadorna cana
Plectropterus gambensis
Pteronetta hartlaubii
Sarkidiornis melanotos
Nettapus auritus
Anas penelope
Anas strepera
Anas crecca
Anas capensis
Anas platyrhynchos
Anas undulata
Anas sparsa
Anas acuta
Anas erythrorhyncha
Anas hottentota
Anas querquedula
Anas smithii
Anas clypeata
Netta erythrophthalma
Aythya ferina
Aythya nyroca
Aythya fuligula
Alcedo semitorquata
Alcedo quadribrachys
Alcedo cristata
Alcedo leucogaster
Megaceryle maxima
Ceryle rudis
Halcyon senegaloides
Centropus grillii
Centropus cupreicaudus
Scotopelia peli
Scotopelia ussheri
Scotopelia bouvieri
Sarothrura pulchra
Sarothrura rufa
Sarothrura lugens
Sarothrura boehmi
Sarothrura ayersii
Himantornis haematopus
Canirallus oculeus
Rallus caerulescens
Crecopsis egregia
Crex crex
Rougetius rougetii
Amaurornis flavirostra
Porzana parva
Porzana pusilla
Porzana porzana
Aenigmatolimnas marginalis
Porphyrio porphyrio
Porphyrio alleni
Gallinula chloropus
Gallinula angulata
Fulica cristata
Fulica atra
Podica senegalensis
Balearica pavonina
Balearica regulorum
Grus virgo
Grus carunculatus
Grus grus
Actophilornis africanus
Microparra capensis
Rostratula benghalensis
Gallinago gallinago
Gallinago nigripennis
Lymnocryptes minimus
Limosa limosa
Limosa lapponica
Numenius arquata
Tringa erythropus
Tringa totanus
Tringa stagnatilis
Tringa nebularia
Tringa ochropus
Tringa glareola
Tringa hypoleucos
Calidris minuta
Calidris temminckii
Calidris alpina
Calidris ferruginea
Philomachus pugnax
Himantopus himantopus
Recurvirostra avosetta
Pluvialis fulva
Pluvialis dominica
Charadrius hiaticula
Charadrius dubius
Charadrius pecuarius
Charadrius tricollaris
Charadrius forbesi
Charadrius pallidus
Charadrius marginatus
Charadrius leschenaultii
Charadrius asiaticus
Vanellus crassirostris
Vanellus armatus
Vanellus spinosus
Vanellus albiceps
Vanellus senegallus
Vanellus gregarius
Vanellus leucurus
Burhinus oedicnemus
Burhinus senegalensis
Burhinus vermiculatus
Pluvianus aegyptius
Glareola pratincola
Glareola nordmanni
Glareola nuchalis
Glareola cinerea
Rynchops flavirostris
Larus ichthyaetus
Larus cirrocephalus
Larus ridibundus
Chlidonias hybridus
Chlidonias leucopterus
Chlidonias niger
Pandion haliaetus
Haliaeetus vocifer
Circus aeruginosus
Circus ranivorus
Circus pygargus
Tachybaptus ruficollis
Podiceps cristatus
Podiceps nigricollis
Anhinga rufa
Phalacrocorax africanus
Phalacrocorax carbo
Phalocrococax capensis
Egretta vinaceigula
Egretta ardesiaca
Egretta garzetta
Ardea cinerea
Ardea melanocephala
Ardea goliath
Ardea purpurea
Casmerodius albus
Mesophoyx intermedia
Bubulcus ibis
Ardeola ralloides
Ardeola idae
Ardeola rufiventris
Butorides striatus
Nycticorax nycticorax
Gorsachius leuconotus

Tigriornis leucolophus
Ixobrychus minutus
Ixobrychus sturmii
Botaurus stellaris
Scopus umbretta
Phoenicopterus ruber
Phoenicopterus minor
Plegadis falcinellus
Bostrychia hagedash
Bostrychia olivacea
Bostrychia rara
Threskiornis aethiopica
Platalea leucorodia
Platalea alba
Mycteria ibis
Anastomus lamelligerus
Ciconia nigra
Ciconia episcopus
Ephippiorhynchus senegalensis
Balaeniceps rex
Pelecanus onocrotalus
Pelecanus rufescens
Laniarius bicolor
Laniarius mufumbiri
Muscicapa cassini
Pseudochelidon eurystomina
Riparia riparia
Riparia paludicola
Riparia congica
Riparia cincta
Phedina brazzae
Hirundo rustica
Hirundo smithii
Hirundo nigrita
Hirundo abyssinica
Cisticola galactotes
Cisticola pipiens
Cisticola carruthersi
Cisticola tinniens
Bradypterus baboecala
Bradypterus carpalis
Bradypterus graueri
Locustella luscinioides
Acrocephalus paludicola
Acrocephalus schoenobaenus
Acrocephalus baeticatus
Acrocephalus arundinaceus
Acrocephalus stentoreus
Acrocephalus griseldis
Acrocephalus rufescens
Acrocephalus gracilirostris
Chloropeta gracilirostris
Motacilla aguimp
Motacilla cinerea
Motacilla clara
Macronyx ameliae
Macronyx grimwoodi
Anthus cervinus
Ploceus subaureus
Ploceus aurantius
Ploceus xanthopterus
Ploceus castanops
Ploceus burnieri
Ploceus taeniopterus
Ploceus spekeoides
Ploceus melanocephalus
Ploceus dicrocephalus
Malimbus nitens
Quelea erythrops
Euplectes franciscanus
Euplectes macrourus
Euplectes hartlaubi
Amblyospiza albifrons
Nesocharis ansorgei
Amandava subflava

APPENDIX 2.4. Pelagic species that do not breed, roost or feed on the subSahara African mainland. Order of listing follows taxonomy presented in Sibley and Monroe (1990)

Family Scolopacidae
Genus Phalaropus
Family Laridae
Genus Catharacta
Genus Stercorarius
Genus Rissa
Family Pelecanidae
Genus Phaetdon
Superfamily Procellarioidea
Family Fregatidae
Genus Fregata
Aptenodytes patagonicus
Eudyptes chrysocome
Eudyptes chrysolophus
Genus Macronectes
Genus Fulmarus
Genus Thalassoica
Genus Daption
Genus Pterodroma
Genus Halobaena
Genus Pachyptylia
Genus Procellaria
Genus Caloanectris
Genus Puffinus
Genus Diomedea
Genus Phoebetria
Genus Oceanites
Genus Pelagodroma
Genus Fregetta
Genus Hydrobates
Genus Oceanodroma
Anous minutus
Anous tenuirostris
Aptendoytes patagonicus
Phalacrocorax coronatus
Phalacrocorax neglectus
Phalaropus fulicarius
Phalaropus lobatus
Sterna fuscata
Sterna paradisaea
Sterna vittata

APPENDIX 2.5. Species that were considered for inclusion in the database, but which were classified as vagrants according to Dowsett & Forbes-Watson (1993). Vagrants are defined as those species that have been only incidentally recorded on the subSahara African mainland. Order of listing follows taxonomy presented in Sibley and Monroe (1990)

Calidris fuscicollis
Calidris melanotus
Calidris ruficollis
Calidris subminuta
Falco columbarius
Gallinago stenura
Haliaeetus albicilla
Larus minutus
Larus sabini
Limnodromus semipalmatus
Steganopus tricolor
Tryngites subrufficollis
Egretta cairulea
Tringa solitaria
Bartramia longicauda
Anthus richardi

APPENDIX 4.1. Estimates of regression coefficients for generalised linear models.

(a) All endemic terrestrial species

	Estimate	s.e.	t(1944)
Constant	221.7	24.9	8.9
TotannR	-0.3119	0.045	-6.93
VarmonR	-0.002847	0.000402	-7.08
SdmonR	1.16	0.128	9.05
CvmonR	-44.93	3.59	-12.5
MaxannT	8.96	7.23	1.24
MeanmonR	3.393	0.558	6.08
CvmaxmonT	-10708	1198	-8.94
MinannT	-14.16	7.19	-1.97
MinmonR	0.293	0.115	2.55
VarminmonT	0.223	0.0523	4.27
SdminmonT	-43.27	4.21	-10.27
sdmonT	63.55	7.88	8.06
absTR	-32.12	7.71	-4.17
SdmonTR	37.03	6.49	5.71
RangeA	0.03563	0.00499	7.14
CvmonTR	1366	246	5.56
Divveg	8.55	1.87	4.58
CvA	275.1	41.9	6.57
SdA	-0.1413	0.028	-5.05
MaxVI	0.6423	0.063	10.19
MinVI	0.687	0.107	6.43
MeanA	0.01482	0.00491	3.02

(b) Endemic passerines

Constant	estimate	s.e.	t(1942)
MeanmonR	70.3	23.6	2.98
VarmonR	2.523	0.56	4.51
SdmonR	-0.001559	0.000262	-5.95
CvmonR	0.254	0.108	2.36
MaxannT	-26.83	2.62	-10.24
TotannR	6.11	3.66	1.67
CvmaxmonT	-0.2266	0.0456	-4.97
SdmaxmonT	-15368	3539	-4.34
MaxmonT	39.5	10.8	3.66
VarminmonT	-11.81	3.66	-3.23
MaxmonT	0.1693	0.0349	4.86
SdmonT	3.37	1.11	3.04
CvmonT	-35.65	8.58	-4.15
CvminmonT	1350	238	5.66
AbsTR	-2673	423	-6.33
CvmonTR	-3.402	0.47	-7.23

RangeA	1955	140	13.95
SdA	0.02028	0.00335	6.05
MeanA	-0.0993	0.0186	-5.35
Divveg	3.344	0.939	3.56
CvA	5.26	1.23	4.27
maxmonR	178.2	28.1	6.34
MinVI	0.1655	0.0366	4.52
MaxVI	0.5142	0.0723	7.11
	0.3456	0.0444	7.78

(c) Endemic nonpasserines

Constant	estimate	s.e.	t(1942)
VarmonR	74.5	10	7.42
SdmonR	-0.001571	0.000157	-9.98
CvmonR	0.4411	0.0906	4.87
MaxmonT	-19.03	1.45	-13.17
CvmaxmonT	-4.99	1.09	-4.58
TotannR	-3479	590	-5.9
MinmonR	-0.1353	0.0228	-5.93
MinmonT	0.1784	0.0548	3.25
MeanmonR	3.046	0.993	3.07
SdmonT	1.373	0.288	4.77
CvminmonT	22.16	2.89	7.66
VarminmonT	-543.2	99.2	-5.48
SdmonTR	0.0465	0.022	2.11
SdminmonT	11.92	1.82	6.56
RangeA	-3.35	2.17	-1.55
AbsTR	0.01057	0.00194	5.45
Divveg	2.657	0.551	4.83
MeanVI	3.619	0.722	5.02
CvA	0.01528	0.00518	2.95
MaxVI	115.9	16.7	6.96
MeanA	0.252	0.0447	5.64
SdA	0.01053	0.00194	5.43
MaxmonR	-0.0423	0.0108	-3.9
CvmonTR	0.0859	0.0255	3.37
	242.1	90.9	2.66

(d) Nonendemic residents

Constant	estimate	s.e.	t(1950)
VarmonR	-25.48	2.6	-9.79
SdmonR	-0.0004979	0.0000591	-8.42
CvmonR	0.2724	0.0298	9.14
MaxmonR	-10.291	0.533	-19.3
VarminmonT	0.03736	0.00893	4.18
MinmonR	-0.08225	0.00792	-10.38

TotannR	0.1454	0.0198	7.33
MaxmonT	-0.023232	0.000985	-23.6
CvmonT	1.5819	0.0889	17.8
RangeA	-60.45	6.43	-9.41
MeanA	0.002921	0.000316	9.23
Divveg	1.869	0.229	8.17
MeanVI	1.925	0.298	6.45
SdminmonT	0.1292	0.0232	5.57
AbsTR	7.72	0.613	12.58
CvVI	-0.748	0.109	-6.86
	16.36	2.32	7.07

(e) All breeding terrestrial species

Constant	estimate	s.e.	t(1945)
MeanmonR	223.2	27.3	8.19
VarmonR	4.012	0.596	6.73
CvmonR	-0.002742	0.000422	-6.49
SdmonR	-56.86	3.87	-14.71
MinmonR	0.587	0.222	2.65
TotannR	0.209	0.143	1.46
CvmaxmonT	-0.387	0.0483	-8.01
MinannT	-13278	1224	-10.85
SdminmonT	-4.181	0.722	-5.79
SdmonT	-36.47	4.19	-8.7
AbsTR	80.65	7.73	10.43
SdmonTR	-27.68	3	-9.23
RangeA	51.39	6.92	7.43
MeanA	0.03572	0.00539	6.62
SdA	0.03412	0.00503	6.78
Divveg	6.17	1.52	4.07
MeanVI	8.9	2.02	4.41
CvA	0.0535	0.0144	3.72
MaxVI	308.6	45.5	6.79
MaxmonR	0.573	0.122	4.68
CvmonTR	0.2997	0.0693	4.32
	781	267	2.92

(f) Non-breeding migrants

Constant	estimate	s.e.	t(1944)
VarmonR	-57.11	7	-8.16
SdmonR	-0.0002161	0.0000769	-2.81
CvmonR	0.2655	0.0236	11.25
MinmonR	-5.756	0.786	-7.32
MaxannT	0.1861	0.0238	7.82
SdmaxmonT	-1.588	0.328	-4.84
MeanmonR	-33.34	3.3	-10.1

CvmaxmonT	0.721	0.125	5.78
TotannR	7131	996	7.16
MinmonT	-0.0789	0.0101	-7.83
SdmonT	4.207	0.301	14
CvVI	33.09	2.34	14.16
CvmonTR	-361.2	42.2	-8.56
RangeA	-381.9	43.4	-8.79
MeanA	0.003703	0.000438	8.46
SdmonTR	0.016745	0.000894	18.73
Divveg	2.193	0.279	7.86
MinVI	1.702	0.368	4.62
MaxVI	0.0412	0.0399	1.03
CvA	-0.0175	0.025	-0.7
VarminmonT	30.05	8.24	3.65
sdVI	-0.02783	0.00945	-2.95
	36.97	6.27	5.9

APPENDIX 5.1. Characteristic and zone-restricted species of terrestrial endemic Afrotropical avifaunal zones.

Northeastern Subregion

CHARACTERISTIC SPECIES (1)

Francolinus leucoscepus.

ZONE-RESTRICTED SPECIES (108)

Acryllium vulturinum, Francolinus psilolaemus, Francolinus harwoodi, Francolinus erckelii, Francolinus ochropectus, Francolinus castaneicollis, Tricholaema melanocephala, Lybius undatus, Trachyphonus erythrocephalus, Trachyphonus darnaudii, Campethera mombassica, Dendropicos abyssinicus, Phoeniculus somaliensis, Tockus flavirostris, Tockus jacksonii, Tockus hemprichii, Colius leucocephalus, Poicephalus flavifrons, Poicephalus rufiventris, Agapornis taranta, Tauraco fischeri, Tauraco leucotis, Tauraco ruspolii, Asio abyssinicus, Caprimulgus onaldsoni , Caprimulgus stellatus, Caprimulgus solala, Columba albitorques, Streptopelia reichenowi, Neotis heuglinii, Eupodotis indiana , Vanellus melanocephalus, Bostrychia carunculata, Lanius cabanisi, Lanius dorsalis, Zavattariornis stresemanni, Corvus rassirostris , Oriolus monacha, Dryoscopus ringlii , Tchagra jamesi, Laniarius ruficeps, Laniarius liberatus, Batis perkeo, Turdus tephronotus, Dioptrornis chocolatinus , Cossypha semirufa , Cercomela dubia, Myrmecocichla melaena, Thamnolaea semirufa , Onychognathus blythii, Onychognathus albirostris, Onychognathus salvadorii, Lamprotornis shelleyi, Speculipastor bicolor, Spreo fischeri, Spreo albicapillus, Cosmopsarus regius, Anthoscopus musculus, Parus leuconotus, Parus thruppi, Hirundo megaensis, Psalidoprocne antinorii, Pycnonotus somaliensis, Cisticola bodessa, Cisticola bodessa, Cisticola cinereolus, Cisticola restrictus, Prinia somalica, Apalis viridiceps, Eremomela flavocrissalis , Turdoides aylmeri, Turdoides squamulatus, Turdoides leucopygius, Parophasma galinieri, Mirafra williamsi, Mirafra hypermetra, Mirafra ashi, Mirafra sharpii, Mirafra alopex, Mirafra poecilosterna, Mirafra degodiensis, Heteromirafra archeri, Heteromirafra sidamoensis, Eremopterix signata, Calandrella erlangeri, Spizocorys personata, Nectarinia tacazze, Nectarinia pembae, Nectarinia nectarinioides, Passer swainsonii, Passer gongonensis, Macronyx flavicollis, Anthus melindae, Plocepasser donaldsoni, Pseudonigrita cabanisi, Ploceus bojeri, Euplectes diadematus, Pytilia lineata, Estrilda ochrogaster, Estrilda charmosyna, Serinus nigriceps, Serinus citrinelloides, Serinus flavigula, Serinus xanthopygius, Serinus donaldsoni, Serinus reichardi, Serinus ankoberensis, and *Emberiza poliopleura.*

Somalia-Masai-Tana-Jubba-Lake-Turkana Province

CHARACTERISTIC SPECIES (7)

Caprimulgus donaldsoni, Speculipastor bicolor, Cosmopsarus regius, Parus thruppi, Prinia somalica, Turdoides aylmeri, and *Emberiza poliopleura.*

ZONE-RESTRICTED SPECIES (29)

Acryllium vulturinum, Colius leucocephalus, Lanius cabanisi, Lanius dorsalis, Dryoscopus pringlii, Tchagra jamesi, Tchagra tchagra, Tchagra perkeo, Turdus tephronotus, Onychognathus salvadorii, Spreo fischeri, Cisticola cinereolus, Apalis viridiceps, Eremomela flavocrissalis, Turdoides squamulatus, Mirafra collaris, Mirafra poecilosterna, Spizocorys personata, Nectarinia permbae, Nectarinia nectarinioides, Passer gongonenesis, Anthus melindae, Plocepasser donaldsoni, Pseudonigrita cabanisi, Ploceus bojeri, Euplectes diadematus, Estrilda charmosyna, Serinus xanthopygius, and *Serinus donaldsoni.*

Somalia-Masai District

CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (7)

Streptopelia reichenowi, Laniarius liberatus, Mirafra ashi, Mirafra sharpii, Mirafra alopex, Mirafra degodiensis, and *Heteromirafra archeri.*

Tana-Jubba District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (3)
Campethera mombassica, Tauraco fischeri, and *Cisticola restrictus.*

Lake Turkana District
CHARACTERISTIC SPECIES (1)
Tockus jacksonii.

ZONE-RESTRICTED SPECIES (5)
Tauraco ruspolii, Zavattariornis stresemanni, Hirundo megaensis, Mirafra williamsi, and *Heteromirafra sidamoensis.*

Ethiopian Highlands Province
CHARACTERISTIC SPECIES (3)
Tauraco leucotis, Bostrychia carunculata and *Corvus crassirostris.*

ZONE-RESTRICTED SPECIES (25)
Francolinus harwoodi, Francolinus erckelii, Francolinus castaneicollis, Dendropicos abyssinicus, Poicephalus flavifrons, Agapornis taranta, Asio abyssinicus, Caprimulgus solala, Columba albitorques, Vanellus melanocephalus, Oriolus monacha, Dioptrornis chocolatinus, Myrmecocichla melaena, Onychognathus albirostris, Parus leuconotus, Psalidoprocne antinorii, Parophasma galinieri, Calandrella erlangeri, Macronyx flavicollis, Pytilia lineata, Estrilda ochrogaster, Serinus nigriceps, Serinus citrinelloides, Serinus reichardi, and *Serinus ankoberensis*

Danakil Province
CHARACTERISTIC SPECIES (0)
ZONE-RESTRICTED SPECIES (1)
Francolinus ochropectus.

Northern Savanna Subregion
CHARACTERISTIC SPECIES (10)
Ptilopachus petrosus, Lybius vieilloti, Dendropicos obsoletus, Macrodipteryx longipennis, Falco alopex, Oenanthe heuglini, Cisticola ruficeps, Turdoides plebejus, Pinarocorys erythropygia, and *Bubalornis albirostris.*

ZONE-RESTRICTED SPECIES (87)
Francolinus schlegelii, Francolinus clappertoni, Francolinus icterorhynchus, Lybius dubius, Lybius rolleti, Campethera punctuligera, Dendropicos elachus, Bucorvus abyssinicus, Coracias cyanogaster, Merops bulocki, Merops nubicus, Poicephalus senegalus, Poicephalus crassus, Tauraco bannermani, Tauraco leucolophus, Musophaga violacea, Caprimulgus eximius, Columba jostedti, Streptopelia hypopyrrha, Streptopelia vinacea, Turtur abyssinicus, Eupodotis savilei, Pterocles quadricinctus, Circaetus pectoralis, Lanius gubernator, Corvinella corvina, Ptilostomus afer, Campephaga phoenicea, Laniarius barbarus, Laniarius atroflavus, Malaconotus gladiator, Batis senegalensis, Platysteira laticincta, Melaenornis edolioides, Cossypha isabellae, Cossypha albicapilla, Myrmecocichla albifrons, Grafisia torquata, Coccycolius iris, Lamprotornis purpureus, Lamprotornis chalcurus, Lamprotornis chloropterus, Lamprotornis caudatus, Lamprotornis pulcher, Anthoscopus punctifrons, Anthoscopus parvulus, Parus guineensis, Hirundo leucosoma, Hirundo domicella, Hirundo preussi, Psalidoprocne mangbettorum, Andropadus montanus, Phyllastrephus poensis, Phyllastrephus poliocephalus, Cisticola rufus, Cisticola troglodytes, Cisticola eximius, Prinia fluviatilis, Drymocichla incana, Urolais epichlora, Apalis bamendae, Eremomela pusilla, Eremomela canescens, Sylvietta brachyura, Mirafra rufa, Galerida modesta, Anthreptes platurus, Nectarinia oritis, Nectarinia coccinigastra, Anthus camaroonensis, Anthus bannermani, Plocepasser superciliosus, Ploceus bannermani, Ploceus luteolus, Ploceus heuglini, Ploceus badius, Malimbus ibadanensis, Nesocharis shelleyi, Nesocharis capistrata, Pytilia phoenicoptera, Pytilia hypogrammica, Euschistospiza dybowskii, Uraeginthus bengalus, strilda caerulescens, strilda troglodytes, Serinus leucopygius, and *Emberiza affinis.*

Central Province
CHARACTERISTIC SPECIES (5)

Merops bulociis, Lamprotornis chloropterus, Cisticola ruficeps, Plocepasser superciliosus, and *Estrilda troglodyte,*

ZONE-RESTRICTED SPECIES (5)
Lybius rolleti, Circaetus pectoralis, Cossypha albicapilla, Lamprotornis purpureus, and *Lamprotornis chalcurus.*

West Central District
CHARACTERISTIC SPECIES (3)
Lybius dubius, Cisticola rufus, and *Estrilda caerulescens.*

ZONE-RESTRICTED SPECIES (4)
Poicephalus senegalus, Musophaga violacea, Streptopelia hypopyrrha, and *Laniarius barbarus.*

East Central District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (1)
Ploceus badius.

Southeastern Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (3)
Poicephalus crassus, Psalidoprocne mangbettorum, and *Lagonosticta umbrinodorsalis.*

Southwestern Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (17)
[CB] = species which, although primarily restricted to the south-western district, also range across the Mt. Cameroon District of the Guineo-Gongolian Subregion as these species occur throughout the Cameroon-Bamenda Highland system which straddles the two aforementioned districts.

Tauraco bannermani, Columba sjostedti [CB], *Laniarius atroflavus* [CB], *Malaconotus gladiator* [CB], *Platysteira laticincta, Cossypha isabellae* [CB], *Coccycolius iris, Andropadus montanus* [CB], *Phyllastrephus poensis* [CB], *Phyllastrephus poliocephalus* [CB], *Urolais epichlora, Apalis bamendae* [CB], *Nectarinia oritis* [CB], *Anthus camaroonensis* [CB], *Ploceus bannermani* [CB], *Malimbus ibadanensis,* and *Nesocharis shelley* [CB].

Species primarily restricted to the Mt. Cameroon District of the Guineo-Gongolian Subregion which stretch into the Southwestern District as they occur throught the Cameroon-Bamenda Highland system:
Zoothera crossleyi, Psalidoprocne fuliginosa, Cisticola discolor, Poliolais lopezi, Phylloscopus herberti, Kupeornis gilberti, and *Nectarinia ursulae.*

Northern Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (1)
Prinia fluviatilis.

Southern Savanna Subregion
CHARACTERISTIC SPECIES (12)
Francolinus afer, Lybius torquatus, Campethera bennettii, Bucorvus leadbeateri, Merops bullockoides, Oriolus larvatus, Campephaga flava, Melaenornis pammelaina, Pinarocorys nigricans, Nectarinia amethystina, Petronia superciliaris, and *Uraeginthus angolensis.*

ZONE-RESTRICTED SPECIES (123)

Francolinus finschi, Francolinus griseostriatus, Francolinus hildebrandti, Francolinus natalensis, Stactolaema leucotis, Stactolaema olivacea, Pogoniulus leucomystax, Pogoniulus simplex, Tricholaema frontata, Lybius melanopterus, Lybius minor, Trachyphonus usambiro, Indicator variegatus, Indicator meliphilus, Campethera abingoni, Tockus alboterminatus, Tockus pallidirostris, Ceratogymna bucinator, Merops nubicoides, Halcyon albiventris, Cercococcyx montanus, Poicephalus cryptoxanthus, Agapornis fischeri, Neafrapus boehmi, Tauraco schalowi, Tauraco erythrolophus, Corythaixoides concolor, Glaucidium capense, Glaucidium scheffleri, Circaetus fasciolatus, Oriolus chlorocephalus, Erythrocercus holochlorus, Trochocercus albonotatus, Trochocercus cyanomelas, Telophorus nigrifrons, Telophorus viridis, Prionops poliolophus, Prionops scopifrons, Batis mixta, Batis dimorpha, Batis fratrum, Batis molitor, Batis soror, Platysteira albifrons, Alethe fuelleborni, Dioptrornis brunneus, Swynnertonia swynnertoni, Sheppardia gunningi, Cossypha anomala, Cercotrichas quadrivirgata, Lamprotornis mevesii, Anthoscopus sylviella, Parus niger, Hirundo nigrorufa, Hirundo rufigula, Psalidoprocne albiceps, Andropadus chlorigula, Andropadus olivaceiceps, Phyllastrephus cabanisi, Phyllastrephus fischeri, Phyllastrephus placidus, Phyllastrephus terrestris, Phyllastrephus cerviniventris, Phyllastrephus flavostriatus, Phyllastrephus debilis, Nicator gularis, Cisticola lepe, Cisticola woosnami, Cisticola nigriloris, Cisticola aberrans, Cisticola rufilatus, Cisticola fulvicapillus, Cisticola angusticauda, Cisticola dambo, Apalis chariessa, Apalis ruddi, Apalis argentea, Apalis kaboboensis, Apalis chapini, Apalis melanocephala, Camaroptera brachyura, Bradypterus mariae, Orthotomus metopias, Orthotomus moreaui, Eremomela salvadorii, Eremomela atricollis, Sylvietta whytii, Macrosphenus kretschmeri, Phylloscopus ruficapillus, Arcanator orostruthus, Turdoides hartlaubii, Turdoides jardineii, Eremopterix leucopareia, Anthreptes neglectus, Anthreptes rubritorques, Nectarinia talatala, Nectarinia ludovicensis, Nectarinia mediocris, Passer suahelicus, Macronyx fuellebornii, Anthus sharpei, Anthus lineiventris, Anthus hoeschi, Anthus sokokensis, Ploceus xanthops, Ploceus bicolor, Euplectes nigroventris, Pytilia afra, Pyrenestes minor, Hypargos margaritatus, Euschistospiza cinereovinacea, Lagonosticta nitidula, Lagonosticta landanae, Lagonosticta rhodopareia, Estrilda perreini, Ortygospiza gabonensis, Lonchura nigriceps, Serinus hypostictus, Serinus citrinipectus, Serinus buchanani, Serinus sulphuratus, Serinus tristriatus, and *Serinus whytii.*

<u>*Brachystegia* Province</u>

* indicates species identified as *Brachystegia* belt zone-restricteds by Benson & Irwin, and [B] indicates species restricted to *Brachystegia* habitat within the *Brachystegia* Province.

CHARACTERISTIC SPECIES (7)

Coracias spatulata, Glaucidium ngamiense, Prionops retzii, Monticola angolensis *[B], *Turdus libonyanus, Myrmecocichla arnotti,* and *Anthoscopus caroli.*

ZONE-RESTRICTED SPECIES (60)

Francolinus shelleyi, Stactolaema anchietae *, *Stactolaema whytii, Tricholaema frontata* *, *Trachyphonus vaillantii, Prodotiscus zambesiae, Campethera scriptoricauda, Tockus bradfieldi* [B], *Tockus pallidirostris* *, *Merops boehmi, Tauraco livingstonii, Musophaga porphyreolopha, Caprimulgus pectoralis, Falco dickinsoni, Lanius souzae* *[B], *Erythrocercus livingstonei, Elminia albicauda, Dryoscopus cubla, Tchagra anchietae, Batis margaritae, Batis molitor, Platysteira peltata, Muscicapa boehmi* [B], *Sheppardia bocagei, Cichladusa arquata, Cercotrichas barbata* *[B], *Lamprotornis elisabeth* *, *Lamprotornis acuticaudus* *, *Neocichla gutturalis* *[B], *Parus rufiventris* *[B], *Parus pallidiventris, Parus griseiventris* *[B], *Hirundo nigrorufa, Psalidoprocne orientalis, Chlorocichla flaviventris, Cisticola melanurus* *, *Apalis alticola, Calamonastes simplex, Calamonastes stierlingi* *, *Eremomela scotops, Eremomela atricollis* *[B], *Sylvietta ruficapilla* *[B], *Phylloscopus laurae, Hyliota australis, Mirafra angolensis, Anthreptes reichenowi, Anthreptes anchietae* *[B], *Nectarinia bannermani, Nectarinia oustaleti* *[B], *Nectarinia manoensis, Nectarinia shelleyi* *[B], *Nectarinia bifasciata, Anthus nyassae, Anthus caffer, Plocepasser rufoscapulatus* *[B], *Ploceus olivaceiceps, Ploceus angolensis* *[B], *Hypargos niveoguttatus, Ortygospiza locustella,* and *Serinus mennelli* *[B].

<u>Drier Zambezian Woodland District</u>

CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (9)
Dendropicos stierlingi, Agapornis lilianae, Agapornis nigrigenis, Alethe choloensis, Pinarornis plumosus, Andropadus milanjensis, Oreophilais robertsi, Apalis chirindensis, and *Ploceus bertrandi.*

Wetter Zambezian Woodland District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (4)
Lybius chaplini, Ploceus katangae, Ploceus ruweti, and *Estrilda nigriloris.*

Zanzibar-Inhambane District
CHARACTERISTIC SPECIES (1)
Batis soror.

ZONE-RESTRICTED SPECIES (3)
Pogoniulus simplex, Batis reichenowi, and *Nectarinia neergaardi.*

Angolan Highlands District
CHARACTERISTIC SPECIES

ZONE-RESTRICTED SPECIES
Francolinus swierstrai, Nectarinia bocagii, and *Ploceus temporalis.*

Central Tanzania District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (4)
Francolinus rufopictus, Apalis kaboboensis, Histurgops ruficauda, and *Ploceus reichardi.*

Zambezian Woodland-Savanna Transitional Province - none.

Eastern Arc Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (36)
Xenoperdix udzungwensis, Agapornis personatus, Otus ireneae, Bubo vosserleri, Lanius marwitzi, Laniarius fuelleborni, Malaconotus alius, Sheppardia sharpei, Sheppardia montana, Sheppardia lowei, Poeoptera kenricki, Lamprotornis hildebrandti, Cinnyricinclus femoralis, Cosmopsarus unicolor, Parus fringillinus, Andropadus masukuensis, Andropadus nigriceps, Cisticola hunteri, Cisticola njombe, Cisticola aberdare, Scepomycter winifredae, Modulatrix stictigula, Turdoides hypoleucus, Turdoides hindei, Calandrella athensis, Anthreptes pallidigaster, Anthreptes rubritorques, Nectarinia loveridgei, Nectarinia moreaui, Nectarinia rufipennis, Ploceus castaneiceps, Ploceus golandi, Ploceus nicolli, Euplectes psammocromius, Euplectes jacksoni, and *Serinus melanochrous.*

Outer Southern Congo Savanna Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (7)
Laniarius brauni, Laniarius amboimensis, Malaconotus monteiri, Prionops gabela, Platysteira albifrons, Sheppardia gabela, and *Camaroptera harterti.*

Tongaland-Pondoland Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (4)
Monticola pretoriae, Cossypha dichroa, Cercotrichas signata, and *Lioptilus nigricapillus.*

Benguela Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (1)
Mirafra naevia.

Guineo-Gongolian Subregion

CHARACTERISTIC SPECIES (43)

Francolinus lathami, Pogoniulus scolopaceus, Pogoniulus subsulphureus, Buccanodon duchaillui, Tricholaema hirsuta, Trachyphonus purpuratus, Campethera nivosa, Eurystomus gularis, Psittacus erithacus, Corythaeola cristata, Accipiter castanilius, Spizaetus africanus, Oriolus nigripennis, Dicrurus modestus, Terpsiphone rufiventer, Laniarius leucorhynchus, Bias flammulatus, Platysteira castanea, Alethe diademata, Alethe castanea, Muscicapa comitata, Andropadus gracilis, Andropadus curvirostris, Baeopogon indicator, Bleda syndactyla, Nicator chloris, Criniger calurus, Eremomela badiceps, Sylvietta virens, Macrosphenus concolor, Hylia prasina, Illadopsis fulvescens, Anthreptes rectirostris, Nectarinia reichenbachii, Nectarinia cyanolaema, Nectarinia superba, Ploceus nigerrimus, Ploceus tricolor, Malimbus malimbicus, Malimbus rubricollis, Nigrita fusconota, Nigrita bicolor, and *Spermophaga haematina.*

ZONE-RESTRICTED SPECIES (182)

Francolinus nahani, Gymnobucco calvus, Gymnobucco peli, Gymnobucco bonapartei, Pogoniulus atroflavus, Indicator maculatus, Indicator conirostris, Melichneutes robustus, Melignomon zenkeri, Prodotiscus insignis, Sasia africana, Campethera caroli, Dendropicos poecilolaemus, Dendropicos elliotii, Phoeniculus bollei, Phoeniculus castaneiceps, Tockus albocristatus, Tockus hartlaubi, Tockus camurus, Tockus fasciatus, Ceratogymna fistulator, Ceratogymna albotibialis, Ceratogymna atrata, Merops gularis, Merops muelleri, Merops malimbicus, Ispidina lecontei, Halcyon badia, Centropus leucogaster, Cercococcyx mechowi, Cercococcyx olivinus, Chrysococcyx flavigularis, Poicephalus gulielmi, Agapornis swindernianus, Telacanthura melanopygia, Rhaphidura sabini, Neafrapus cassini, Apus batesi, Tauraco schuetti, Tauraco macrorhynchus, Otus icterorhynchus, Bubo poensis, Bubo shelleyi, Bubo leucostictus, Jubula lettii, Glaucidium tephronotum, Glaucidium sjostedti, Glaucidium castaneum, Caprimulgus binotatus, Caprimulgus nigriscapularis, Columba unicincta, Columba albinucha, Columba iriditorques, Turtur brehmeri, Dryotriorchis spectabilis, Accipiter erythropus, Urotriorchis macrourus, Smithornis sharpei, Smithornis rufolateralis, Pitta reichenowi, Oriolus brachyrhynchus, Coracina azurea, Campephaga petiti, Campephaga oriolina, Dicrurus atripennis, Erythrocercus mccallii, Trochocercus nigromitratus, Trochocercus albiventris, Trochocercus nitens, Dryoscopus senegalensis, Dryoscopus angolensis, Dryoscopus sabini, Laniarius luehderi, Laniarius poensis, Telophorus bocagei, Telophorus multicolor, Malaconotus cruentus, Malaconotus lagdeni, Prionops rufiventris, Bias musicus, Batis ituriensis, Batis occulta, Platysteira tonsa, Platysteira blissetti, Platysteira chalybea, Platysteira jamesoni, Platysteira concreta, Neocossyphus fraseri, Neocossyphus rufus, Neocossyphus poensis, Zoothera cameronensis, Zoothera princei, Alethe poliocephala, Fraseria ocreata, Fraseria cinerascens, Muscicapa infuscata, Muscicapa olivascens, Muscicapa sethsmithi, Muscicapa epulata, Muscicapa tessmanni, Myioparus griseigularis, Stiphrornis erythrothorax, Sheppardia poensis, Sheppardia cyornithopsis, Cossypha roberti, Cossypha cyanocampter, Cercotrichas leucosticta, Cercotrichas hartlaubi, Poeoptera lugubris, Onychognathus fulgidus, Lamprotornis purpureiceps, Anthoscopus flavifrons, Pholidornis rushiae, Parus funereus, Andropadus ansorgei, Andropadus gracilirostris, Andropadus latirostris, Calyptocichla serina, Ixonotus guttatus, Chlorocichla simplex, Thescelocichla leucopleura, Phyllastrephus lorenzi, Phyllastrephus albigularis, Phyllastrephus icterinus, Phyllastrephus xavieri, Bleda eximia, Criniger chloronotus, Criniger ndussumensis, Prinia leucopogon, Prinia bairdii, Apalis nigriceps, Apalis binotata, Apalis personata, Apalis rufogularis, Camaroptera superciliaris, Camaroptera chloronota, Bradypterus alfredi, Bathmocercus rufus, Eremomela badiceps, Eremomela turneri, Sylvietta denti, Macrosphenus flavicans, Hyliota violacea, Illadopsis cleaveri, Illadopsis albipectus, Illadopsis puveli, Illadopsis rufipennis, Kakamega poliothorax, Phyllanthus atripennis, Anthreptes fraseri, Anthreptes gabonicus Nectarinia seimundi, Nectarinia batesi, Nectarinia reichenbachii, Nectarinia fuliginosa, Nectarinia rubescens, Nectarinia bouvieri, Nectarinia chloropygia, Nectarinia minulla, Nectarinia johannae, Ploceus pelzelni, Ploceus weynsi, Ploceus albinucha, Ploceus preussi, Ploceus dorsomaculatus, Malimbus flavipes, Malimbus coronatus, Malimbus cassini, Malimbus scutatus, Malimbus malimbicus, Brachycope anomala, Parmoptila rubrifrons, Parmoptila woodhousei, Nigrita bicolor, Nigrita luteifrons, Nigrita canicapilla, Spermophaga poliogenys, Spermophaga haematina, Estrilda nonnula, Estrilda atricapilla, Lonchura bicolor, and *Serinus frontalis.*

Congolian Province

CHARACTERISTIC SPECIES (4)

Accipiter toussenelii, Terpsiphone rufocinerea, Nicator vireo, and *Anthreptes aurantium.*

ZONE-RESTRICTED SPECIES (16)

Guttera plumifera, Agelastes niger, Gymnobucco sladeni, Dendropicos gabonensis, Dendropicos xantholophus, Apaloderma aequatoriale, Merops breweri, Centropus anselli, Caprimulgus batesi, Picathartes oreas, Hirundo

fuliginosa, Psalidoprocne petiti, Baeopogon clamans, Anthus pallidiventris, Malimbus racheliae, and *Malimbus erythrogaster.*

Central District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (3)
Afropavo congensis, Apalis goslingi, and *Nectarinia congensis.*

Disjunct District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (3)
^{E} = species confined to the eastern portion and ^{W} to the western portion of the disjunct district.

Centropus neumanni ^{E}, *Bradypterus grandis* ^{W}, and *Ploceus batesi* ^{W}.

Gabon District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (1)
Ploceus subpersonatus.

Mt. Cameroon District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (4)
Francolinus camerunensis, Telophorus kupeensis, Speirops melanocephalus, and *Bradypterus lopezi.*

Inner Southern Congo Savanna District
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (1)
Cossypha heinrichi

Guinea Province
CHARACTERISTIC SPECIES (4)
Dendropicos lugubris, Neocossyphus finschii, Criniger barbatus, and *Macrosphenus kempi.*

ZONE-RESTRICTED SPECIES (5)
Melignomon eisentrauti, Prionops caniceps, Muscicapa ussheri, Phyllastrephus baumanni, and *Nectarinia adelberti.*

Lower Guinea District - none.

Upper Guinea District
CHARACTERISTIC SPECIES (3)
Agelastes meleagrides, Picathartes gymnocephalus, and *Lamprotornis cupreocauda.*

ZONE-RESTRICTED SPECIES (10)
Campethera maculosa, Ceratogymna cylindrius, Campephaga lobata, Melaenornis annamarulae, Phyllastrephus leucolepis, Prinia leontica, Apalis sharpei, Bathmocercus cerviniventris, Illadopsis rufescens, and *Malimbus ballmanni.*

Ubangi-Uelle Savanna Province - none

Albertine Rift Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (47)
Species restricted to the Albertine rift mountains are denoted $^{\wedge}$, and Lake Victoria zone-restricteds are denoted ^{LV}

Francolinus nobilis [^], *Indicator pumilio* [^], *Schoutedenapus schoutedeni* [^], *Musophaga johnstoni* [^], *Glaucidium albertinum* [^], *Phodilus prigoginei* [^], *Caprimulgus prigoginei* [^], *Pseudocalyptomena graueri* [^], *Coracina graueri* [^], *Terpsiphone bedfordi* [^], *Prionops alberti* [^], *Batis diops* [^], *Zoothera tanganjicae* [^], *Zoothera oberlaenderi* [^], *Zoothera kibalensis* [^], *Alethe poliophrys* [^], *Melaenornis ardesiacus* [^], *Muscicapa lendu*, *Muscicapa itombwensis* [^], *Sheppardia aequatorialis*, *Cossypha archeri* [^], *Parus fasciiventer* [^], *Andropadus kakamegae*, *Chlorocichla laetissima*, *Chlorocichla prigoginei* [^], *Phyllastrephus hypochloris*, *Cisticola chubbi*, *Apalis ruwenzorii* [^], *Graueria vittata* [^], *Sylvietta chapini* [^], *Hemitesia neumanni* [^], *Phylloscopus laetus* [^], *Phylloscopus budongoensis*, *Kupeornis rufocinctus* [^], *Kupeornis chapini* [^], *Nectarinia alinae* [^], *Nectarinia stuhlmanni* [^], *Nectarinia regia* [^], *Nectarinia rockefelleri* [^], *Nectarinia purpureiventris* [^], *Anthus latistriatus*, *Ploceus alienus* [^], *Ploceus victoriae* [LV], *Ploceus aureonucha*, *Cryptospiza jacksoni* [^], *Cryptospiza shelleyi* [^], and *Serinus koliensis* [LV].

Southwestern Subregion

CHARACTERISTIC SPECIES (12)

Colius colius, *Pterocles namaqua*, *Cursorius rufus*, *Melierax canorus*, *Batis pririt*, *Myrmecocichla formicivora*, *Sylvia subcaeruleum*, *Eremopterix verticalis*, *Passer melanurus*, *Sporopipes squamifrons*, *Serinus flaviventris* and *Emberiza impetuani*.

ZONE-RESTRICTED SPECIES (64)

Francolinus africanus, *Francolinus levaillantoides*, *Francolinus capensis*, *Francolinus adspersus*, *Tricholaema leucomelas*, *Campethera notata*, *Geocolaptes olivaceus*, *Poicephalus rueppellii*, *Agapornis roseicollis*, *Apus bradfieldi*, *Neotis ludwigi*, *Eupodotis afra*, *Eupodotis rueppellii*, *Eupodotis vigorsii*, *Eupodotis caerulescens*, *Grus paradisea*, *Pterocles burchelli*, *Circus maurus*, *Buteo rufofuscus*, *Lanioturdus torquatus*, *Laniarius atrococcineus*, *Telophorus zeylonus*, *Monticola rupestris*, *Monticola explorator*, *Monticola brevipes*, *Bradornis infuscatus*, *Bradornis mariquensis*, *Sigelus silens*, *Oenanthe monticola*, *Cercomela schlegelii*, *Cercomela tractrac*, *Onychognathus nabouroup*, *Spreo bicolor*, *Anthoscopus minutus*, *Parus cinerascens*, *Parus afer*, *Pycnonotus nigricans*, *Pycnonotus capensis*, *Cisticola subruficapillus*, *Prinia flavicans*, *Malcorus pectoralis*, *Zosterops pallidus*, *Stenostira scita*, *Eremomela gregalis*, *Turdoides melanops*, *Turdoides bicolor*, *Turdoides gymnogenys*, *Sylvia layardi*, *Mirafra cheniana*, *Mirafra apiata*, *Mirafra sabota*, *Certhilauda curvirostris*, *Chersomanes albofasciata*, *Eremopterix australis*, *Spizocorys conirostris*, *Spizocorys fringillaris*, *Eremalauda starki*, *Nectarinia fusca*, *Passer motitensis*, *Philetairus socius*, *Estrilda thomensis*, *Amadina erythrocephala*, *Serinus albogularis*, and *Serinus leucolaema*.

Fynbos-Karoo-Highveld Province

CHARACTERISTIC SPECIES (2)

Cercotrichas coryphaeus and *Galerida magnirostris*

ZONE-RESTRICTED SPECIES (7)

Eupodotis afraoides, *Eupodotis vigorsii*, *Cercomela sinuata*, *Prinia maculosa*, *Certhilauda albescens*, *Anthus crenatus*, and *Serinus alario*.

Highveld District

CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (2)

Chaetops aurantius and *Serinus symonsi*.

Karoo District

CHARACTERISTIC SPECIES (2)

Euryptila subcinnamomea and *Spizocorys sclateri*.

ZONE-RESTRICTED SPECIES (2)

Phragmacia substriata and *Certhilauda burra*.

Fynbos District

CHARACTERISTIC SPECIES (5)

Turnix hottentotta, *Bradypterus victorini*, *Promerops cafer*, *Nectarinia violacea*, and *Serinus totta*.

ZONE-RESTRICTED SPECIES (2)

Chaetops frenatus and *Serinus leucopterus*.

Kalahari Province
CHARACTERISTIC SPECIES (1)
Calamonastes fasciolatus.

ZONE-RESTRICTED SPECIES (8)
Francolinus hartlaubi, Tockus monteiri, Poicephalus rueppellii, Cercotrichas paena, Namibornis herero. Lamprotornis australis, Achaetopus pycnopygius, and *Certhilauda chuana*.

Namib Province
CHARACTERISTIC SPECIES (0)

ZONE-RESTRICTED SPECIES (2)
Certhilauda erythrochlamys and *Certhilauda barlowi*.

Northern Arid Subregion
Northern Province- none

Horn of Africa Province
CHARACTERISTIC SPECIES (1)
Sylvietta philippae.

ZONE-RESTRICTED SPECIES (6)
Columba oliviae, Buteo archeri, Mirafra somalica, Alaemon hamertoni, Spizocorys obbiensis, and *Carduelis johannis*.

APPENDIX 6.1. Red Data categorisation of Afrotropical species according to Collar *et al.* (1994).

Species name	RD category
Agelastes meleagrides	VU
Francolinus camerunensis	VU
Francolinus swierstrai	VU
Francolinus ochropectus	CR
Francolinus harwoodi	VU
Francolinus griseostriatus	VU
Afropavo congensis	VU
Xenoperdix udzungwensis	EN
Melignomon eisentrauti	VU
Schoutedenapus schoutedeni	VU
Tauraco bannermani	VU
Tauraco ruspolii	EN
Otus ireneae	VU
Glaucidium albertinum	VU
Columba oliviae	VU
Grus paradisea	VU
Larus leucophthalmus	VU
Falco fasciinucha	VU
Gyps coprotheres	VU
Geronticus calvus	VU
Pseudocalyptomena graueri	VU
Campephaga lobata	VU
Laniarius amboimensis	EN
Laniarius brauni	EN
Telophorus kupeensis	CR
Malaconotus alius	CR
Malaconotus gladiator	VU
Malaconotus monteiri	EN
Prionops alberti	VU
Prionops gabela	EN
Prionops poliolophus	VU
Platysteira laticincta	VU
Picathartes gymnocephalus	VU
Picathartes oreas	VU
Zoothera guttata	EN
Alethe choloensis	VU
Melaenornis annamarulae	VU
Muscicapa lendu	VU
Swynnertonia swynnertoni	VU
Sheppardia gabela	EN
Sheppardia gunningi	VU
Sheppardia lowei	VU
Sheppardia montana	VU
Cossypha heinrichi	VU
Cinnyricinclus femoralis	VU
Hirundo atrocaerulea	VU
Hirundo megaensis	VU
Chlorocichla prigoginei	VU
Phyllastrephus leucolepis	CR
Bleda eximia	VU
Criniger olivaceus	VU
Prinia leontica	VU
Apalis argentea	VU
Apalis bamendae	VU
Apalis chariessa	VU
Apalis karamojae	VU
Speirops melanocephalus	VU
Bathmocercus cerviniventris	VU
Scepomycter winifredae	VU
Orthotomus moreaui	CR
Eremomela turneri	VU
Macrosphenus pulitzeri	EN
Arcanator orostruthus	VU
Turdoides hindei	EN
Kupeornis gilberti	VU
Mirafra ashi	EN
Mirafra degodiensis	VU
Heteromirafra archeri	EN
Heteromirafra ruddi	CR
Heteromirafra sidamoensis	EN
Certhilauda burra	VU
Spizocorys fringillaris	VU
Anthreptes pallidigaster	VU
Anthreptes rubritorques	VU
Nectarinia rockefelleri	VU
Nectarinia rufipennis	VU
Anthus chloris	VU
Anthus sokokensis	VU
Ploceus aureonucha	VU
Ploceus bannermani	VU
Ploceus batesi	VU
Ploceus golandi	VU
Ploceus nicolli	VU
Ploceus nigrimentum	VU
Ploceus subpersonatus	VU
Malimbus ballmanni	EN
Malimbus ibadanensis	CR
Cryptospiza shelleyi	VU
Estrilda nigriloris	VU
Estrilda poliopareia	VU
Carduelis johannis	EN